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PEST CONTROL BY CHEMICAL, BIOLOGICAL, GENETIC, AND PHYSICAL MEANS

A Symposium

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PEST CONTROL BY CHEMICAL, BIOLOGICAL, GENETIC, AND PHYSICAL MEANS

A Symposium

Chairman

E. F. KNIPLING
Agricultural Research Service
U.S. Department of Agriculture

Participants

Personnel of the Canada Department of Agriculture,
U.S. Department of the Interior, U.S.
Department of Agriculture, University of
Western Ontario, U.S. State Universities,
and Industry

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PEST CONTROL BY CHEMICAL, BIOLOGICAL, GENETIC, AND PHYSICAL MEANS

A Symposium

INTRODUCTION

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Pest control is necessary to provide the food, fiber, and other agricultural items required by the expanding world population. It is also essential to control the many arthropod vectors that transmit devastating diseases to man, such as malaria, typhus, and plague.

The role that pesticides can take in improving the welfare of mankind throughout the world has been clearly demonstrated during the past two decades--a period during which hundreds of new insecticides, herbicides, nematocides, fungicides, and other pesticides came into extensive use.

It would be difficult to appraise accurately the benefits to mankind that have already accrued as the result of the many new chemical weapons available for the control of pests. It would likewise be difficult to imagine the adverse impact on man's future welfare and economy if we could not rely on the use of these valuable chemical agents or did not know of alternate ways to control pests. People tend to forget the past and accept new developments as a matter of fact. However, in dealing with pest problems, people must maintain constant vigilance to meet new situations and to maintain the advances that have been made.

As valuable as pesticides have been, their increased use has resulted in some complex problems because of side effects they can produce to many beneficial nontarget organisms in our environment. Most pesticides, especially those designed to destroy animal pests--invertebrates or vertebrates--can be expected to be hazardous to at least some other animal species if exposed to the pesticide. Past basic knowledge has permitted development of only a few chemicals sufficiently selective in basic action or sufficiently selective in manner of use to destroy the target pest without creating hazards to other animals in the same general environment. This does not mean that progress has not been made in selective use of pesticides. Such progress will be pointed out by the scientists who will discuss certain pesticides and methods of using them against both vertebrate and invertebrate pests. Although there has been progress, in most instances we do not yet have the materials and methods to achieve the degree of selectivity that we would like to have.

From an overall viewpoint, a great deal can be said about our progress in employing pesticides without leaving high-level residues in our food supply. It is somewhat surprising, moreover, that the many highly toxic pesticides have been employed without creating more hazards to people that handle them in comparison with the hazards of common drugs, household chemicals of many kinds, common industrial chemicals, and similar substances. At the same time, much can be said about the known and potential adverse impact of pesticides for the control of certain pests without exposing other organisms in the same environment to the spray or to the residues that may remain. Free-ranging organisms cannot be excluded from sprayed areas. All the pesticide applied in a given environment may not remain in that environment.

A thorough study of the pesticide problem by the President's Science Advisory Committee, which culminated in the report on "The Use of Pesticides," placed the major issues in their proper perspective. In essence this report stated that we need to control pests to provide for man's needs and to protect him from vector-borne diseases, but it also pointed out that there are known hazards and potentially grave risks associated with the extensive use of certain pesticides of the type now available and in the manner in which they are currently employed.

In developing this symposium, the planning committee decided that nothing could be gained by discussing the controversial aspects of pesticide use. Millions of words covering various aspects of the controversy are now in print, often written by extremists. Dozens of scientific symposia have been held by many organizations to discuss the pros and cons of the use of pesticides. All this has been of value in pointing out the problems. It has long been the writer's view that merely discussing issues will not solve the problems we face.

Much of the public may accept risks in the use of pesticides in view of their benefits. However, the public would rather achieve effective pest control without risks to the environment. People often cannot agree on relative values--it all depends on circumstances as they are affected or on their personal sense of values. The public demands clean, high-quality, unblemished foods at reasonable prices. People desire virtual freedom from annoyance or threats to their health that pests can cause. At the same time they would like to have all these things without risks to themselves or to their environment. When there is no alternative, men of responsibility must weigh the risks of the pest versus the risk of the pest-control measures that can be employed. In the meantime, however, if there is a reasonable chance through research to develop ways of controlling our more important pests with little or no hazard to man or his environment, there is every justification for an all-out effort to achieve this objective.

Accordingly, this symposium was designed to consider the opportunities for controlling pests of all kinds without creating undue risks to man and his environment. The symposium is a broad one--pest control by all the various means we now know--chemical, biological, genetic, and physical. It encompasses all the major kinds of invertebrate and vertebrate pests of agricultural importance--insects, plant diseases, weeds, and nematodes, as well as birds and mammals in situations where they become pests.

Many approaches to pest control have been investigated in the past. Only those methods that have led to practical achievements, however, are well known. For too many years, research on agricultural pests has emphasized short-term applied research. Due to the thousands of pest problems, many of day-to-day urgency, most available research resources were devoted to developing quick solutions to problems of an emergency nature. Moreover, research on chemical pesticides for many years was recognized as offering the best chance of finding a satisfactory solution to most pest problems. Research in this area, especially during the past two decades, was backed by the competence and great resources of our chemical industries. Thus, research efforts on chemical pesticides, both public and private, were far greater than on other potentially useful methods.

Scientists have continued to make significant progress, however, on other approaches to the problems of pest control in relation to the effort devoted to the research. Plant geneticists working with plant pathologists, entomologists, and nematologists have made outstanding progress in solving several pest problems. Scientists who have continued to work on natural biological control agents have shown new opportunities for more effective use of insect diseases, insect parasites, and predators. Important new leads have been obtained on ways to affect the behavior of pests as the result of research on natural materials in the pests themselves or in the hosts on which they live. Outstanding advances in methodology in the chemical field have greatly improved opportunities for identifying these substances. Along this same line, progress has been made by the relatively few scientists who have been exploring various physical factors that affect the behavior of vertebrate and invertebrate pests.

During the past two decades, the possibility of employing pests themselves for self-destruction by utilizing the sterility principle has begun to emerge. Ways to employ pest-control measures that have a maximum impact on a total population of insects instead of mere segments of populations have also emerged. Such innovations may lead to more efficient application of the pest-control weapons we already have or may develop in the future.

In view of new developments and the recognition of new opportunities to deal with pest problems, it appeared that the time was appropriate to organize a symposium that would bring together scientists of various disciplines to consider the current status and future opportunities of various methods of pest control.

Outstanding authorities in specific fields of work were invited to participate in and lead the symposium sessions. Two outstanding scientists and administrators of research programs will discuss topics of broad scope related to all the specific topics included in the program.

PEST CONTROL BY CHEMICAL MEANS

A. W. A. Brown, Department of Zoology,
University of Western Ontario

Whereas the emphasis in pest control research is now being placed on biological means, to which Dr. Knipling has given a new look by pioneering the sterility principle for insect control and eradication, yet the main burden of combating pests is at present carried on principally by chemical means. Far from having reached a status quo, research in chemical control is pushing forward on all fronts. The development of very sensitive methods of detecting traces of insecticides in animal tissues, in alerting us to the possible dangers of their accumulation in the food chain, has diverted public attention from the remarkable successes that have been attained with chemical pesticides in agriculture and world health and blinded us to the fact that they are being used with increasing safety.

Dr. Metcalf, whose knowledge of insecticide development is unrivaled, is struck by the slowness of agriculture to adopt many improvements that research has already made known, for example the substitution of the more biologically-labile and less residue-prone compounds among the organophosphates or even the chlorinated hydrocarbons. Dr. Shaw, perhaps taking a leaf from Dr. Metcalf's book, recommends the development and testing of new herbicides on a rational basis, by exploring within a range of chemical analogs with known biological action. Dr. Dykstra urges that all promising biologically active compounds be tested for their possible usefulness as piscicides, avicides, or rodenticides. We can detect here the interaction taking place between these groups of investigators, providing instances of that interdisciplinary research which Dr. Glen so ably commends and describes.

Again we are taken by the scruff of our necks and carried forward by Dr. Beroza, who states that good insect sex attractants lie all around us just waiting to be isolated for use as baits for insecticides and chemosterilants, thus offering the possibility for controlling insects by chemical means without generally contaminating the environment. Dr. Howell would have us make our livestock insectproof by putting something clever in their food and drink. Dr. McNew, not satisfied with the excellent and safe performance of present-day fungicides, would have us learn more about the biochemistry of fungus spores so that we can design more perfect chemical weapons. But Dr. Good, who has to undertake his search for suitable nematocides right from the beginning, will take his active toxicants wherever he can find them, even if it comes to an organophosphorus insecticide or a nitrogenous herbicide like atrazine.

These are the people who get on with the job, for the control of pests is becoming an increasingly important commitment as the human population further expands.

THE NEED FOR INTERDISCIPLINARY RESEARCH IN PEST CONTROL

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The welfare of man is seriously challenged by the fantastic rate at which his numbers are increasing. Control of births, provision of food, and prevention of human disease must all receive greater attention in the immediate future, if present standards of living are to be raised or even maintained. In the short run, we are not likely to achieve a radical reduction of births in the developing countries. Nor can we deliberately retard medical progress. Therefore, we must expect a rising world demand for more food and less disease. Pest control is vital to both objectives. But pest-control measures affect the environments on which man is dependent for essential raw materials. Man's well-being is likely to depend, in no small way, on the long-range effects of those pest-control practices, which he will be forced to use in greater and greater measure in the next two decades to sustain the exploding human population.

An understanding of the effects of such control measures can be gained only through research. The purpose of this paper is to examine the general character of the pest problem in the above context and the research needed, with special consideration of the interdisciplinary aspects.

SOME GUIDELINES

The term "pest control" is used here in the broad sense. In essence, pest includes any organism that competes with man for essential food or shelter or that transmits human pathogens. Control is the attainment of practical protection from such pests. In pest control, we are usually concerned with pest abundance rather than the mere presence of the species; and with local infestations of distinct geographical and physiological races rather than the species as a whole. Thus, the basic unit in pest control is the population of an identifiable subspecies, race, strain, or variety of noxious organism. This concept is well illustrated in plant pathology by differences in pathogenicity in races of cereal rusts, in entomology by differences in DDT resistance in strains of the house fly, and in agronomy by differences in tolerance to many factors in varieties of crops and weeds.

Pest control has been pursued with great diversity and ingenuity. To make the point, I need only mention such devices as pesticides, parasites, predators, disease organisms, resistant varieties of crops and breeds of animals, tillage practices, crop rotations, pasture management, cutting and pruning regimes, flooding, draining, fertilizers, hormones, chemosterilants, sterile male technique, physical and chemical attractants and repellents, controlled storage and transport facilities, and various combinations of these measures. The list could be lengthened. But it is surely clear that to combat pests man deliberately modifies his environment.

This is not surprising, for man's chief preoccupation has been, and is, with his environment and particularly with modifying it to his own advantage. He has been pursuing this course since he first evolved and has finally succeeded in wresting the control of his own future from the traditional and slower forces of evolution that previously shortened his life and limited his numbers. Now man is controlling and changing his environment to fit his special needs (1). He has made remarkable progress in preventing disease and in providing food and shelter. As a result, his numbers have increased dramatically. The present situation is such that if the current rate of human increase continues, the world population will double in about 35 years, but only if we can produce enough food to sustain such numbers. This achievement will require prudent use of our natural resources.

Here then is the broad setting in which we should contemplate the nature and future of pest control: As the effective management of pest populations without reducing the inherent productivity of the environments concerned. In its long-term aspects, such pest control is essentially an exercise in applied ecology. In this context, the use of pesticides and parasites and other pest-control measures are simply factors to be assessed, continued, or discarded in our development and exploitation of natural and manmade ecosystems for the provision of food and shelter and protection from disease-carrying vectors.

BASIC INTERRELATIONS AFFECTING PEST CONTROL

Interdependence is a universal law, well known to ecologists. Each organism has its own genetic code; but it is the environment that supplies the energy and materials which the inherited DNA guides into the formation of living tissues and life processes. As Platt et al. (2) suggested: "It seems useful to think of the environment-organism relationship as one having no arbitrary boundaries and in which flow rates and transfer rates between the organism and its environment are of paramount importance." To understand these relationships is a formidable task, but this is the ultimate goal of ecology. Whether it be in the ocean, forest, wheatfield, greenhouse, or warehouse, the impact of the total environment will determine whether any organism or population will succeed, merely survive, or fail. And this universal fact applies alike to beneficial and pest populations, whether or not man has intervened, and whether or not he has deliberately introduced a pest-control measure. In this paper we are only concerned with pest control, but this restriction in no way changes the basic fact: Pest control cannot be adequately assessed in isolation; it must be studied in relation to the other elements of the communities concerned.

Most of the outdoor environments in which pest control is practiced are complex and dynamic. In such instances, pest abundance is affected by physical factors, such as light, heat, moisture, fire, and atmospheric composition, pressure, and motion; by biotic factors, such as food, disease organisms, parasites, competitor species, and inherent development and behavior patterns that confer various degrees of protection against adverse forces; and by manmade components, such as pesticides, lures, and cropping practices. The importance of any given factor varies in relation to other factors that are concurrently active. It is not the individual factor, therefore, but the whole complex of factors that normally controls populations. But so-called catastrophic mortality factors (3) have been known to reduce insect populations to insignificant proportions in a remarkably short time. Fire, storms, epidemics of disease, and applications of chemicals fall in this category.

Suffice it to say that ecology in general and pest control, as a form of applied ecology, demand the simultaneous attention of many kinds of scientists. The need for interdisciplinary research is obvious in a field of science that is, to quote Edward Deevey (4), "more multidisciplinary than any other."

But an adequate pest-control program rests on a still broader base than orthodox ecology. In entomology, for example, we need continuing support from the undergirding fields of anatomy, taxonomy, physiology, genetics, and behavior; and from studies of speciation, competition, parasitism, and adaptation. As stated by Glen (5): "These can be undertaken by individual entomologists or by laboratories or institutions devoted primarily or solely to a study of insects. But when we undertake to study the interrelations of insects with agriculture, forestry, commerce, or public health, much more than entomology is involved and the traditional entomology laboratory must give place to the broader-based research station embracing all the relevant disciplines and functioning under the authority of a single director." Such a changeover occurred in the Canada Department of Agriculture in 1959 and a similar shift is projected for the Canada Department of Forestry. Interdisciplinary approaches to pest-control problems in both fields will receive greater attention as a result of this change in organization. The point to be emphasized here is that the change grew out of experience and the eventual conviction that many practical problems of farming and forestry, including pest control, are very much broader than is the training of the individual research specialists required for their solution.

The use of pesticides is but one of a growing array of pest-control methods. But the "pesticide problem," in its grosser aspects, is known to cross scientific boundaries, to involve several levels of government, to affect both primary and secondary industries, and to both benefit and threaten the welfare of plants, animals, and man. The same boundlessness characterizes the problem at the other extreme, the cellular and molecular level. Here chemists and physiologists work to relate chemical structure and toxicity and to elucidate modes of action while geneticists probe the phenomenon of resistance. Between these extremes is a vast middle ground where engineers, physicists, and meteorologists strive to get better pesticide coverage; entomologists, plant pathologists, agronomists, and economists struggle to determine when pesticide use is justified; and ecologists and mathematicians attempt to develop sampling and analytical techniques appropriate to the populations being studied. Much the same order of diversity characterizes the field of biological and other methods of control and, of course, the use of combined or integrated control measures, which is bound to receive more and more attention in the future. It is easy to see why we have come to recognize such hybrid specialties as biochemistry, biophysics, biometeorology, biomathematics, and, finally, biogeochemistry. These significant developments provide further testimony that training in restricted disciplines is insufficient to meet the research problems of today. Highly trained specialists are indispensable in modern research; but for applied research in depth, teams of such specialists are commonly needed.

EXPERIENCE FROM CHEMICAL CONTROL

The use of pesticides illustrates some of the complexities inherent in the development and administration of pest-control programs. We should profit from this experience in looking ahead, especially since there is every likelihood that the use of pesticides will be continued indefinitely into the future.

In the last two decades, the use of pesticides has provided billions of dollars' worth of food and fiber and prevented countless human illnesses. But the lavish use of such a variety of toxic substances in so many different formulations and under so many different environmental conditions has raised a question that cannot be fully answered: What is the long-term hazard to man's productive environments and to man himself of continuing this practice?

Public interest has been widely aroused. Agriculturists, foresters, and health authorities are well aware of the advantages achieved. They remain the principal users and, in general, the main supporters for continuation of pesticide use, albeit with increased precautions for safety. Those responsible for the production of fish and wildlife and for other conservation programs are more fearful of the consequences and less anxious to see chemical control continued on the current scale. The chemical industries are directly involved, of course, and the lay public has expressed itself variously and vigorously.

Governments have introduced statutory safeguards at both the regional and federal levels in most advanced countries to require registration of pesticides before sale, to limit specific uses of certain compounds, and to regulate the amount of pesticide permitted in food entering commercial markets. The question of food contamination extends into international trade and carries with it, among others, a need for international agreement on methods for measuring pesticide residues. Such analytical techniques have advanced spectacularly in recent years. Now we can detect the presence of many compounds in parts per billion or even per trillion. This refinement means that products may now be declared "contaminated," which previously, by less sensitive methods, would have been certified free of residues. This change greatly complicates the administration of official residue tolerances, especially where regulations permit no contamination. The confusion arises from the fact that in many instances our ability to detect the presence of a pesticide has outstripped our capacity to interpret the significance of the amount found.

With few exceptions, it is impracticable to experiment directly on humans. Consequently, both acute and chronic toxicity of a compound to man have to be gaged from studies with experimental animals. This approach has acknowledged weaknesses. Nevertheless, the record so far has been remarkably good. I am not aware of any human poisonings as a result of the marketing of food contaminated with pesticides. The Food and Drug Regulations appear to be providing adequate safeguards in this regard. But in addition to problems in human toxicology, many other important problems confront us: The development of pesticide-resistant strains of pests; the persistence of different compounds in different environments and their uptake from different types of soil by different kinds of plants under different weather conditions; the movement of pesticides within and between ecosystems and their concentration in the food chain; the synergistic effects on different animals and man of different pesticides with other chemicals; and the effect of small doses of toxicants consumed over several generations on fertility, vigor, and survival of susceptible forms of birds and animals;--to name but a few.

This grossly incomplete account will at least indicate the welter of conflicting circumstances, uncertainties, and difficulties under which we must continue to develop chemical control measures. Clearly there is need for constant vigilance and for a more comprehensive program of research. But there is no cause fo pessimism.

Cooperative planning points the way. But first we need a meeting of minds from all the sectors of society concerned with the pest and pesticide problem, particularly from agriculture, forestry, fisheries, wildlife, and public health, to establish mutual understanding and confidence. Jointly they must survey the problem, compile records of research in course, determine mutual and independent spheres of interest, reach agreement on major goals, and select priorities for future study.

The decisions should be integrated at regional and national levels and finally internationally into a combined effort to use available resources to best advantage. We must strive for complementary instead of duplicatory programs both intranationally and internationally. Even then, operations will have to be confined to a small number of the enormous possibilities for research that confront us. One has only to reflect on the innumerable kinds of soils, crops, animals, pests, chemicals, husbandry practices, and weather that are involved to realize that critical selection of projects is mandatory. Properly trained personnel, suitable research facilities, and funds are all in short supply; and, whether we like it or not, we must plan the program to fit these limitations. But plan we must. And let us willingly breach those scientific and administrative barriers that in the light of our collective wisdom should be and can be breached.

Each country must work out its own approach to this problem. In Canada we are presently striving to develop the necessary liaison. In 1964, the Federal Government formed an Interdepartmental Committee on Pesticides with representation from seven Federal agencies. This advisory body reports to the Minister of Agriculture and is charged with keeping the whole pesticide problem in Canada under regular review. The formation of counterpart advisory committees in each Province is under consideration. On this organizational framework we hope to develop a cooperative and coordinated approach to such complex long-range issues as legislation, research, and major control operations.

Helpful experience is already available from the Interdepartmental Committee on Forest Spraying Operations (6), which has been functioning in Canada since 1958. This is an operational committee with membership from Federal forestry, fisheries, and wildlife interests. It represents the Government of Canada in joint planning of cost-sharing pest-control programs with provincial government departments and industrial associations and agencies. The objectives of the Committee are to review important forest insect problems that may require control by forest spraying; to coordinate the views of different agencies concerned with control projects and their consequences; to review research needs and to promote research investigations relevant to lessening risks to other forms of life affected by operational programs; and to insure that the same information on control projects, hazards, etc., is transmitted to the senior officials of each of the Federal departments concerned. The Committee has dealt with a number of projects and programs, the largest being the spraying of several million acres for spruce budworm control in New Brunswick (7). As a result of shared experiences and cooperative research, the operational program has been repeatedly modified in an effort to serve the interests of all concerned with the total productivity of the region. This experience has strengthened our confidence in the value of interdisciplinary research and joint management in dealing with major pest-control problems.

Collaborative approaches to the pesticide problem are also well advanced in other countries, notably the United States (8) and the United Kingdom (9); and the international Organization for Economic Cooperation and Development (OECD) is considering a conference to assess the problem of environmental contamination from pesticides on a still wider geographic scale. Undoubtedly a further stimulus to interdisciplinary research will arise from these deliberations. Certainly the achievement of intermanagement planning is prerequisite to the full development of interdisciplinary science.

OTHER CONSIDERATION

The development of science is part of our cultural evolution. Its division into disciplines, faculties, kinds of research, etc., is temporary and subject to change. And change it must as we accumulate new knowledge and increase our understanding of nature. Neither knowledge nor nature is truly divisible and this fact, of itself, lends support to giving greater and greater emphasis in the future to interdisciplinary research in any field.

There is also a need to balance developments in broad complementary fields of research, if man's best interests are to be served. For example, too little notice has been given hitherto to the interdependence of medicine and agriculture. As John Rust (10) said, "...saving lives and improving health through medical practice are only meaningful if agriculture can keep pace and supply the food needed to maintain the life and health of those saved. Medical and agricultural sciences ... must increasingly work as a team if they are to serve mankind fully." Then he added this important point: "In any cold analysis of the recent advances and developments in the medical and agricultural sciences, it is quite apparent that medicine leads." This he explained on the basis that medical science, "in its artful practice," is applicable to a wider variety of world situations than is agricultural science. Sir William Slater (1) in discussing problems in colonial development concluded that agricultural progress presented a much more difficult and complicated task than the improvement of public health. This disparity between essential human needs is most pronounced in the less developed countries, where agricultural science has had a relatively smaller impact. To redress such imbalance will require assessment of all major research programs at the highest levels nationally and internationally and a mutual willingness to define and support long-range objectives in terms of the common good.

A promising start has already been made in this direction. Several of the advanced nations now have special advisory science committees and ministers, or other senior government appointees, for the development and coordination of their science programs. Just this year, Canada established a Scientific Secretariat to advise the Prime Minister on such matters. And in 1963, OECD convened the first meeting of Ministers for Science to share experiences in developing national science programs and to discuss intergovernment collaboration.

PROGNOSIS

These significant events when combined with the lessons gleaned from pest control and other complex problems provide an augury for the future. Our scientific and cultural evolution appears to have reached the point where some long-established concepts, prerogatives, and procedures are becoming outmoded. As the tempo of scientific discovery increases, our organization for research must be updated with increasing frequency to serve better the purpose for which it exists. At any rate, the sanctity of organization must not be permitted to impede scientific progress. Independence and isolation must gradually give place to interdependence and collaboration. More attention should be given to the development of attitudes and administrative arrangements that will provide the flexibility of operations appropriate to our rapidly changing circumstances.

The new circumstances that will shape our future will arise as problems that generate strong public pressures within countries and among countries and demand a fresh approach; problems that might well suggest that it is more important to have an adequate total national program with respect to them than to maintain inflexible and independent research roles for universities, governments, and industries; problems that might force us to share with sister departments or other countries the mammoth task of conducting essential investigations. Such problems are not likely to involve entire disciplines or fields of endeavor, such as all entomology or all agriculture, but rather parts of several disciplines and of several sectors of society.

Many facets of the pest-control problem fit these stipulations. It is within this broader context that we can expect interdisciplinary research in pest control to increase. The interdisciplinary approach is simply the mark of maturity. It is our new frontier and we must meet its challenge or retard progress.

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REQUIREMENTS FOR INSECTICIDES OF THE FUTURE

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The control of insect pests with chemicals has a relatively short history. A tea from powdered tobacco was used to destroy plant lice in 1763, crushed Chrysanthemum flowers, containing the pyrethrins, were used to control fleas and lice in about 1800, and ground roots of Derris were used against leaf-eating caterpillars in 1848. The first synthetic insecticide was paris green or copper acetoarsenite applied to control the Colorado potato beetle in about 1865. Potassium dinitro-o-cresylate was marketed as an insecticide in Germany in 1892, and the appearance of β-butoxy-β'-thiocyanodiethyl ether in 1932 marked the beginning of the era of large-volume use of synthetic organic pesticides. During the next three decades more than 100 insecticides and acaricides have become commercial items, and annual sales in the United States now exceed $200 million.

Insecticides have become an indispensable adjunct of modern agriculture, providing unblemished fruits and vegetables and often materially increasing crop yields. Through such innovations as seed treatments, soil fumigations, and animal systemics, they have become an integral part of mechanized crop production. In the area of public health, insecticides have virtually eliminated the horrors of plague, typhus, yellow fever, and malaria, and they provide the basic weapons for the control of encephalitides and filariasis. The householder has become an enthusiastic customer of mothproofed woolens, lawn and garden sprays, and the ubiquitous (90 million units per year) "bug bomb."

With the increasing appreciation for and sophistication of the use of pesticides has come professional (35) and public (4) awareness of the problems inherent in their indiscriminate and overenthusiastic application. These problems may be grouped into three broad categories:

(1) The lack of appropriate pesticide selectivity between pest and man and his domestic animals, between pest and wildlife, and between destructive and beneficial insects.

(2) The selection by continued use of a pesticide of resistant races or strains, so that the pesticide ultimately loses much of its usefulness.

(3) The lack of environmental degradability for certain persistent pesticides, so that these accumulate in soil and within plant and animal tissues, where they are subject to ecological magnification by food-chain organisms.

This symposium surveys current knowledge of the status of pest-control practices, with the goal of providing insight into nonchemical means to control pests of all descriptions. At the same time, it is unrealistic to imagine that it will be possible in the foreseeable future to feed and clothe the world's expanding population and to preserve present standards of health and hygiene without recourse to the use of chemical pesticides. Therefore, there are three important avenues of approach to the safe and proper utilization of these chemicals: (1) Employment of pesticides only when required as emergency control measures for pest populations that are producing injury beyond the economic threshold; (2) establishment of conditions for pesticide usage based on minimal dosages and the most suitable formulations, timing, methods, and sites of application; and (3) development of new pesticides and methods of application that are far more selective and far more free from problems of environmental contamination than those presently in widescale use.

SELECTIVE TOXICITY OF INSECTICIDES

The definition of the word insecticide "an agent for destroying insects" clearly implies selectivity of action, since the human user certainly does not intend to share equally with his intended arthropod victim in the hazards of unrestricted chemical warfare. Equally, he does not expect that his normal use of plant sprays will harm foliage or fruits or that applications to livestock will be deleterious to animal health. Nevertheless, many substances used to kill insects are inherently hazardous to higher animals, and their selectivity is apparent only through careful application and confinement to the treated area. Examples include hydrogen cyanide as a fumigant, parathion as a dust or spray, and arsenic trioxide as a poisoned bait.

Progress has been made in improving the selective action of these generally toxic insecticides by localizing them precisely to the area needing treatment and by combining them in baits or with specific attractants so as to bring the pest to the poison. Examples include the use of lindane or dieldrin in seed treatment at 0.25 ounce per acre to replace a broadcast application of 2 pounds per acre; the incorporation of the specific attractant methyl eugenol with parathion in bait boxes to annihilate male oriental fruit flies (Dacus dorsalis) and the incorporation of dichlorvos (dimethyl 2,2-dichlorovinyl phosphate) or naled (dimethyl 1,2-dibromo-2,2-dichloroethyl phosphate) at 1 percent in granulated sugar as a bait for house flies to replace general residual sprays. The development of systemic insecticides, which when applied to seeds or as granular preparations about plant roots enter into the plant translocation stream and are concentrated into leaves and fruits, has provided an important avenue for controlling plant-feeding pests without damage to their natural parasite and predator enemies and had led to the development of ecological selectivity. Much additional research remains to be accomplished in this general area of improving the selectivity of intrinsically nonselective materials by selective application and utilization.

It is, however, in the discovery of insecticides that are truly selective in a physiological and biochemical way that the chemist and toxicologist have the greatest opportunity to produce the genuinely sophisticated and desirable insecticides of the future. We shall consider some of our present knowledge of selectivity as it relates to the development of narrow-spectrum insecticides of low toxicity to higher animals and with a wide margin of safety to beneficial pollinators, parasites, and predators. The fundamental aspects of such selective action will also lead us to considerations of the most fascinating area of selectivity between susceptible and resistant races of the same species.

Selectivity by Restricted Absorption

From many viewpoints, the DDT-type insecticides can scarcely be improved upon as selective insecticides. The data of table 1 illustrate the inability of DDT and methoxychlor to penetrate the selective barrier of the mammalian cuticle. However, for the house fly and the cockroach, absorption through the insect cuticle is extremely efficient, so that the external and internal lethal dosages are virtually equivalent. This is, however, not the case for all insects--the LD_{50} for the grasshopper (*Melanoplus differentialis*) is 9,380 mg. per kilogram topically and 2 mg. per kilogram injected (22). Other types of insecticides are readily absorbed by the mammalian cuticle as shown by the high cutaneous toxicity of parathion to the rat (table 2).

Very little careful study seems to have been made of the physiological and biochemical phenomena involved in the selective rejection or acceptance by the living cuticle of insects and mammals. Since cuticular absorption is, under conditions of normal use, the most important avenue for the ingress of insecticides, investigations in this area should be particularly rewarding in the development of selective insecticides.

Selective Toxicity of Parathion-Type Compounds

Parathion (*O,O*-diethyl *O*-*p*-nitrophenyl phosphorothioate) was the first of the broad-spectrum organophosphorus insecticides, and its discovery by Schrader (37) marked an important milestone in the development of insecticides. The use of this material and its dimethyl analog has grown by leaps and bounds, and it is estimated that approximately 20 million pounds of these materials are produced annually. Because of their low cost and high degree of insecticidal activity, the parathion compounds continue to represent the most efficient insecticides available. However, as shown in table 2, parathion is one of the least

Table 1.--Selective toxicity of DDT and methoxychlor (29)

[LD_{50} mg. per kg.]

Insecticide	Rat				*Musca*, topical	*Periplaneta*	
	Oral	Cutaneous	I.p.	I.v.		Topical	Injected
DDT.................	200	3,000	150	45	6.0	10	7
Methoxychlor....	6,000	>6,000 (rabbit)	--	--	15	--	18

Table 2.--Comparative toxicity of parathion and malathion (29)

[LD_{50} mg. per kg.]

Insecticide	Rat				*Musca domestica*, Topical	*Periplaneta americana*, injected	Protoparce *sexta*, topical
	Oral	Cutaneous	I.p.	I.v.			
Parathion........	3	45	4	3	1.4	1.0	2.8
Malathion........	1,500	> 4,000	750	50	28	8.4	23.6

selective of all insecticides, and its casual use by uninstructed personnel is hazardous. The dimethyl analog of parathion has a higher degree of insect selectivity, but this is far from optimal. However, several simple derivatives of this type of compound have an amazing degree of insect selectivity as shown in table 3.

Although these parathion analogs have had some use as insecticides for specific purposes, especially in the household or on animals, they are generally more specific in their action than parathion. This characteristic and their considerably greater cost have unfortunately limited their application.

More recently two other types of safer parathion-type materials have appeared, which promise better insect selectivity together with broader scale utility. The employment of the methylthio group as a potential activating (electron withdrawing) group for the phenyl dialkyl phosphates was described by Fukuto and Metcalf (9). They showed that the subsequent in vivo oxidation of the methylthio moiety to sulfoxide and sulfone was a type of lethal synthesis in the animal organism. The paraoxon and parathion-type derivatives incorporating this group have been found to be highly effective as insecticides and nematocides and to possess systemic insecticidal action. However, they have little or no selective toxicity to insects (2). Schrader (36) showed that the incorporation of a methyl group *ortho* to the methylthio group as in fenthion (*0,0*-dimethyl *0*-3-methyl-4-methylthiophenyl phosphorothioate) produced a remarkable increase in insect selectivity. This selectivity was expanded to truly dramatic proportions by the addition of two *ortho*-methyl groups.

Nishizawa et al. (30) made the equally valuable discovery that the insecticidal specificity of methyl parathion could be greatly improved by the similar incorporation of an *ortho*-methyl group. The resulting compound 'Sumithion' ('Folithion', *0,0*-dimethyl *0*-3-methyl-4-nitrophenyl phosphorothioate) appears to be a highly versatile insecticide with a greatly reduced mammalian toxicity (table 3). Careful biochemical studies have not revealed dramatic differences between the processes of intoxication and detoxication with Sumithion and methyl parathion. The studies suggest that Sumi-oxon (P=O) is relatively a better inhibitor of insectan than mammalian cholinesterase and that Sumithion and Sumi-oxon may be somewhat more rapidly detoxified in mammals. The net effects of the several differences in rates of reaction are toxicity for insects and safety to mammals.

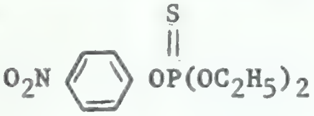
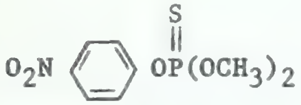
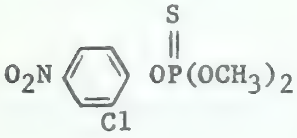
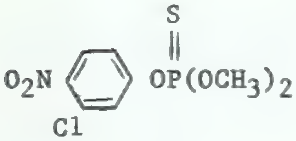
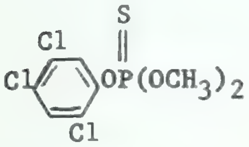
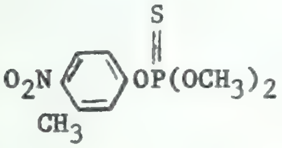
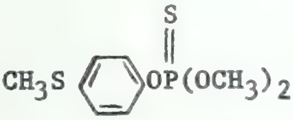
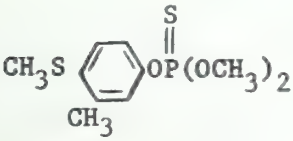
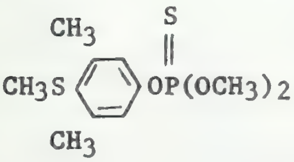
Selectivity to Beneficial Insects

It has been said most aptly (21) that "there is no doubt that the greatest single factor in keeping plant-feeding insects from overwhelming the rest of the world is that they are fed upon by other insects." The importance of this insect internecine warfare is well recognized by entomologists, as indicated by much of the context of this symposium, and chemical control measures for insects are generally to be regarded as emergency measures to be applied only where biological equilibria have failed to curtail pest numbers below economic thresholds. The concept of integrated control (40) therefore involves the application of specific or selective pesticides in a manner that will supplement or augment the activities of beneficial insects. Selective insecticides will also have a major role in protecting the honey bee and a variety of other wild bees, syrphid flies, and other pollinating insects, which are indispensable in helping the farmer to produce more than $4,500 million worth annually of our commonest fruits and vegetables.

These types of selective action appear to be entirely feasible. There are ways, i.e., by the application of systemic insecticides to plant roots and through the use of toxic baits, whereby broad-spectrum insecticides may be rendered highly specific. This discussion, however, is more properly concerned with the intrinsic selectivity of toxicants by virtue of their chemical properties and the biochemical capacity of both pest and beneficial organisms. As an example of possibilities, the behavior of isopropyl parathion (*0,0*-diisopropyl *0*-*p*-nitrophenyl phosphorothioate) is interesting. A number of years ago the writer noted that this close relative of the broad-spectrum insecticide parathion (*0,0*-diethyl *0*-*p*-nitrophenyl phosphorothioate) was virtually nontoxic to the honey bee, although it was highly toxic to the house fly. Subsequent study (24) showed that the selectivity of isopropyl parathion extended to the *Opius* parasites of the oriental fruit fly (*Dacus dorsalis*), which was

Table 3.--Selective toxicity of parathion analogs (23)

[LD_{50} mg. per kg.]

Parathion anolog	Rat, oral	Rabbit, cutaneous	House fly, topical
	6	45	0.9
	15	350	1.3
	475 (mouse)	2,000 (guinea pig)	1.6
	1,500	--	11.5
	1,740	1,500	2.75
	500	3,000	2.6
	10	--	2.0
	500	400	2.3
	3,000	--	4.3

more than 100 times as suceptible on a weight basis.

The data in table 4 show that the remarkable selectivity to the bee is confined to the diisopropyl phosphorothioate ester. Biochemical investigations have shown that this selectivity is the net result of the inability of the bee to readily accomplish the lethal synthesis of diisopropyl *p*-nitrophenyl phosphate from the phosphorothioate (a microsomal oxidation) coupled with the lower affinity of the phosphate metabolite for bee cholinesterase. The conjunction of these two variances in reaction rates suffices to provide a difference of approximately 1,000-fold in the ultimate rates of diisopropyl phosphorylation between the fly enzyme and bee enzyme. Field trials of isopropyl parathion to ascertain the extent of its selective action would seem to be warranted.

Selectivity of Malathion and Related Compounds

The development in 1950 of malathion (*O,O*-dimethyl *S*-(1,2-dicarbethoxyethyl) phosphorodithioate) was an important milestone in the emergence of the selective toxicity of the organophosphorus insecticides (14). An interesting comparison between the selectivity of malathion and the nonselectivity of parathion is shown in table 2. Since that time the comparative use of millions of pounds of both materials on a worldwide basis has indicated that malathion can be applied without appreciable hazard to human or animal health, whereas parathion, unless carefully handled by trained personnel, may cause illness and even death. Therefore, although parathion is from 2 to 20 times more active to insects than malathion, the latter has had increasingly widespread application as a general-purpose insecticide for use by the general public (38).

Inquiry into the biochemical basis for the selectivity of malathion should provide a rationale for the development of other selective insecticides. Animals poisoned by malathion show symptoms of anticholinesterase activity, yet purified malathion is not an anticholinesterase. It is apparent that malathion (P=S) is oxidized in vivo into mala-oxon (P=O), which is about 1,000 times as active as an anticholinesterase. The oxidizing enzyme system is found in the microsomal fraction of mouse liver and in cockroach midgut and fat

Table 4.--Selectivity of parathion derivatives to house fly and honey bee (24)

Parathion derivative	Topical LD_{50} γ per gram		Selectivity ratio bee/fly
	Fly	Bee	
$O_2NC_6H_4OP(S)(OMe)_2$	1.2	0.84	0.7
$O_2NC_6H_4OP(S)(OEt)_2$	.9	3.5	3.9
$O_2NC_6H_4OP(S)(OPr)_2$	4.0	14.8	3.7
$O_2NC_6H_4OP(S)(OiPr)_2$	4.2	>1,000	> 240
$O_2NC_6H_4OP(S)(OBu)_2$	120	530	44
$O_2NC_6H_4OP(O)(OMe)_2$	1.5	1.0	.7
$O_2NC_6H_4OP(O)(OEt)_2$	1.2	.6	.5
$O_2NC_6H_4OP(O)(OPr)_2$	9.0	4.0	.4
$O_2NC_6H_4OP(O)(OiPr)_2$	7.5	5.0	.7
$O_2NC_6H_4OP(O)(OBu)_2$	75	114	1.5

body. The comparative toxicities and anticholinesterase activities of malathion and mala-oxon, which are much less selective, are shown in table 5.

In addition to the activation oxidase system, malathion and mala-oxon are degraded in both mammals and insects by carboxyesterase, which removes one of the ethyl ester groups, leaving compounds that are not anticholinesterases because the phosphorus atom is no longer highly electrophilic. Further degradation of the malathion-type molecules also occurs. The complete metabolic scheme in insects and mammals is shown in figure 1.

Table 5.--Comparison of malathion and mala-oxon (31)

Insecticide	LD_{50} mg. per kg.			I_{50} ChE *M*.	
	Mouse, i.p.	*Musca*, topical	*Periplaneta*, topical	Mouse brain	Fly brain
Malathion..........	1,590	28	16	4.2×10^{-5}	2.0×10^{-5}
Mala-oxon..........	75	15	1.5	4.0×10^{-8}	4.6×10^{-9}

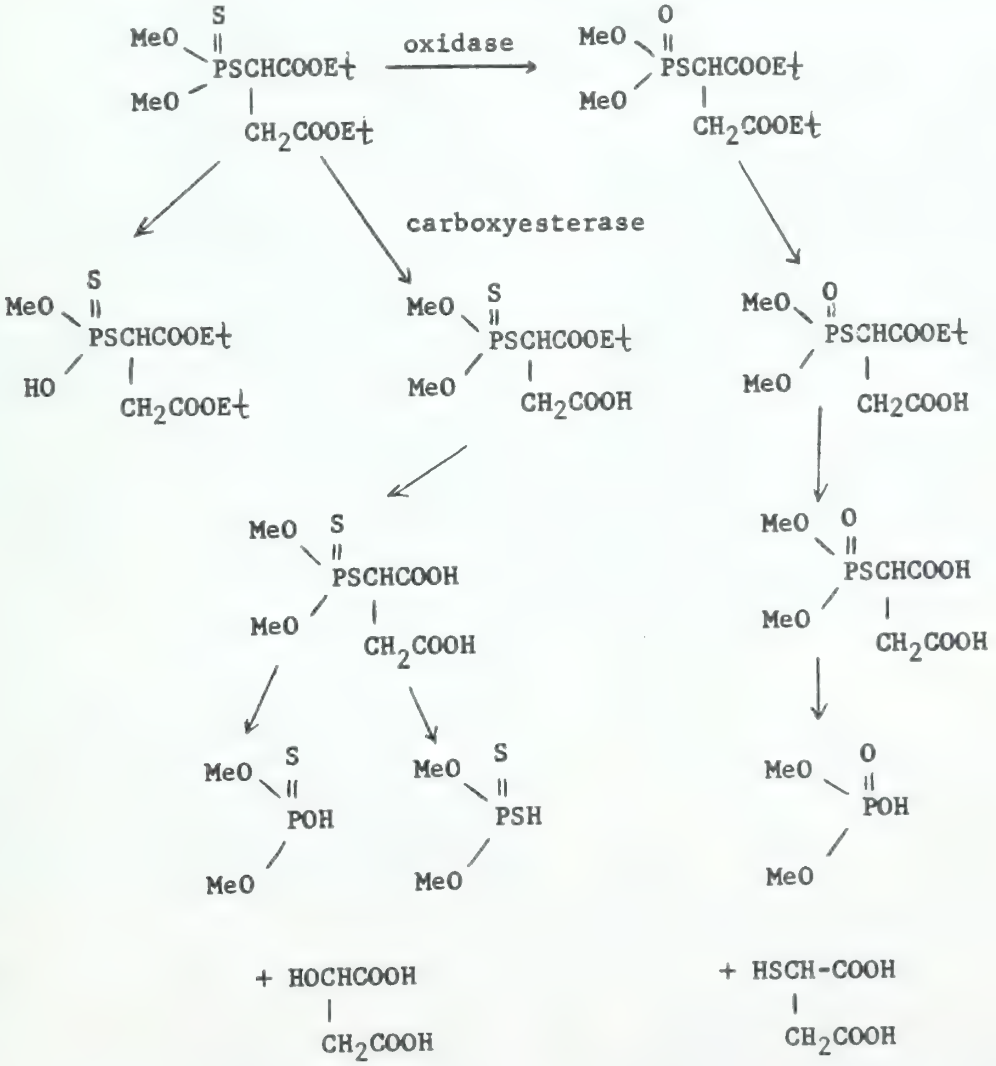


Figure 1.--Metabolic pathways of malathion in insects and vertebrates.

Krueger and O'Brien (15) have shown that when mice and cockroaches are injected with 30 mg. per kilogram of radioactive malathion, mala-oxon levels after 2 hours were approximately 10 times as high in the cockroach as in the mouse. March et al. (18) and O'Brien (31) found that radioactive malathion was much more rapidly and extensively metabolized in the mouse than in the cockroach. Thus it appears that the highly selective action to insects is the overall result of more rapid lethal synthesis in the insect and more rapid detoxication in the mammal.

Confirmation of this hypothesis has come about in a most interesting way through the work of Frawley and associates (8) on the possible synergistic or potentiating effects of simultaneous exposure of mammals to malathion and EPN (O-methyl O-p-nitrophenyl phenylphosphorothioate). The individual and combined toxicities for these materials in a 25:1 ratio are shown in table 6. It is evident that a marked degree of synergism was observed. In extensive biochemical investigations of this phenomenon, DuBois (7) found that the intravenous injection of rats with EPN at 1.5 mg. per kilogram decreased, after 1 hour, the mala-oxon detoxifying capacity of the liver by 84 percent and of the blood serum by 93 percent. This dosage of EPN also decreased the LD_{50} of malathion from 1,100 to 550 mg. per kilogram. Additionally it was shown (table 7) that relatively small amounts of dietary EPN would inhibit the enzymatic destruction of mala-oxon in rats. This suggested to DuBois that TOCP (tri-o-cresyl phosphate), which is well known as an aliesterase inhibitor, should also potentiate malathion. It was found that TOCP (i.p. LD_{50} 2,500) when given to rats at 110 mg. per kilogram decreased the LD_{50} of malathion, given 24 hours later, from 1,100 alone to 8.2 intraperitoneally.

Table 6.--Potentiation of toxicity of malathion by EPN (8)

[LD_{50} mg. per kg.]

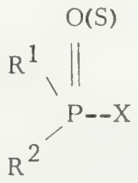
Insecticide	Rat, oral
Malathion..................	1,400
EPN........................	65
Malathion (25) plus EPN (1)	167 + 6.6
(Expected additive values).	700 + 32.5

Table 7.--Effect of dietary EPN on mala-oxonase in rats (28)

EPN(p.p.m.)	Inhibition mala-oxonase	
	Liver	Serum
	Percent	Percent
5............	28	39
10...........	57	59
20...........	78	81
50...........	88	91
100..........	95	95

From these experiments it seems clear that the low toxicity of malathion to mammals is due to the high rate of carboxyesterase detoxication of both malathion and its activation product mala-oxon by the mammalian liver. This principle of selectivity can undoubtedly be applied to many other molecules. O'Brien et al. (33) have produced a group of highly selective carboxyester derivatives of diethylphosphoric acids. Acethion ($(C_2H_5O)_2P(S)SCH_2COOC_2H_5$) had an i.p. LD_{50} to the mouse of 1,280 and a topical LD_{50} to the fly of 9.4 mg. per kilogram. Its selectivity was much greater than that of the more toxic P=O derivative acetoxon, demonstrating the importance of the delay factor (P=S oxidation) in providing an opportunity for enzymatic detoxication in the mammal.

From this discussion of selectivity of organophosphorus insecticides, it may be concluded that careful molecular tailoring can produce O-P molecules with nearly any desired type of selectivity. The number of O-P compounds with insecticidal action is incredibly large. From the basic structure for toxic action (Schrader 37)



and our knowledge of the allowable diversity of R^1: CH_3O-$C_8H_{17}O$; CH_3S-$C_8H_{17}S$; CH_3NH-C_4H_9NH, CH_3-C_3H_7 = >50,

R^2: CH_3O-C_3H_7O; CH_3S-C_3H_7S;

CH_3-C_8H_{17} = 50,

and the displaceable group X: more than 10,000 different moieties incorporating electron withdrawing groups or groups that can be enzymatically activated to this state (50 x 50 x 10,000 = 25 million combinations), it appears that at least 25 million potential insecticides can be fabricated around this simple phosphorylating structure. Within this enormous framework and fortified with some basic concepts of the nature of insecticidal specificity between mammals and insects, parasites and hosts, and susceptible and resistant organisms, planned organic synthesis should be able to achieve almost any desirable goal.

Selectivity of Carbamates

These compounds are esters of *N*-methyl or *N*,*N*-dimethylcarbamic acid and a variety of phenols and heterocyclic enols. Like the organophosphorus insecticides they are inhibitors of cholinesterase, but because of their close spatial similarity to acetyl choline they may also have a direct stimulating effect on acetyl choline receptors.

The carbamates are among the most selective of all insecticides both in their differential toxicity to insects and vertebrates and in their specific action among the arthropods. One of the interesting features of this specificity is the pronounced effect of formal charge of the molecule in preventing insecticidal action. Prostigmine while extremely toxic to mammals is inactive as a contact insecticide, although it is a very active inhibitor (I_{50} 2 x 10^{-8} M) of both insect and mammalian cholinesterase. However, its uncharged carbon isosteres, such as *m*-isopropylphenyl and *m*-tert-butylphenyl *N*-methylcarbamates, are toxic to both insects and mammals (table 8).

A considerable amount of study has indicated that cationic compounds, such as prostigmine and acetyl choline, are unable to penetrate the lipoid sheath that surrounds insect nerves. However, in mammals these compounds, although they may not penetrate the central nervous system, act peripherally where they block neuromuscular transmission and cause death by respiratory impairment. The failure

Table 8.--Selectivity of some carbamate insecticides

[LD_{50} mg. per kg.]

Insecticide	*Musca*, topical	*Blattella*, topical	*Apis*, topical	Rat, oral	Rabbit, dermal
m-Dimethylaminophenyl *N*,*N*-dimethylcarbamate methobromide (prostigmine)...............	5,000	--	--	7.5	--
m-Isopropylphenyl *N*-methylcarbamate.........	90	14	0.1	16	>600
o-Isopropylphenyl *N*-methylcarbamate.........	105	>130	2.8	300	>3,000
o-Isopropoxyphenyl *N*-methylcarbamate........	22.5	11.3	.8	100	>800
1-Naphthyl *N*-methylcarbamate (carbaryl).....	900	>130	2.3	540	>5,000
2-Methyl-2-methylthiopropionaldehyde oxime *N*-methylcarbamate........................	6.0	--	--	1.0	5.0
1-Isopropyl-3-methyl-5-pyrazolyl *N*,*N*-dimethylcarbamate (Isolan).................	75	--	--	11.0	--

of cationic compounds to produce peripheral effects in insects suggests along with other very limited data that insect myoneural junctions are not cholinergic. Thus, the cationic carbamates represent the converse of selective insecticides--selective mammalicides.

Some of the carbamates developed as insecticides, such as Isolan (1-isopropyl-3-methyl-5-pyrazolyl N,N,-dimethylcarbamate) and 2-methyl-2-methylthiopropionaldehyde oxime N-methylcarbamate, are highly toxic to both mammals and insects (table 8). However, many of the newer N-methylcarbamate insecticides not only are of low or moderate oral toxicity to mammals but also are virtually nontoxic by cutaneous application. Carbaryl (Sevin), one of the safest of the groups, has passed all tests as a dusting powder for body lice, where it is used in conjunction with piperonyl butoxide synergist.

In regard to chronic toxicity, the carbamates are particularly suitable. These esters are very labile and are readily detoxified and excreted as conjugated aryl sulfates and glucuronate. Carbaryl, for example, has been fed to rats at 200 p.p.m. without any effect or any tissue storage. When residues are ingested by dairy cattle, carbaryl is not concentrated and secreted in butter fat as is DDT. The metabolism of carbaryl, as shown in figure 2, is an excellent example of desirable pesticide biodegradability. The principal metabolic pathways are hydroxylation of ring and N-methyl groups by microsomal oxidases and hydrolysis by aliesterase action. These detoxication pathways account for the often unexpected selective action of the carbamate insecticides to insects. Examples are shown in table 8.

Unfortunately the honey bee and other Hymenoptera are extremely susceptible to carbaryl and other carbamates and appear to lack the microsomal oxidases that are abundant in the house fly, for example. These detoxifying enzymes are very susceptible to inhibition by the methylenedioxyphenyl compounds, such as piperonyl butoxide, which synergizes carbaryl as much as 400-fold in the female house fly. One of the newest carbamate synergists is 2,3-methylene-dioxynaphthalene, which gives appreciable synergism with carbaryl when present at one one-hundredth part (Metcalf, R. L., unpublished data).

INSECT RESISTANCE TO INSECTICIDES

Acquired resistance of insects to insecticides is another manifestation of selective toxicity. The resistance arising through natural selection depends in most cases on enhanced ability of the organism to detoxify the insecticide, and the biochemical defense mechanisms are exactly the same sort that afford protection to higher animals. Although resistance is a natural consequence of the ability of organisms to detoxify an almost unlimited variety of chemical compounds present in their food and environment, its occurrence poses challenging problems in the development of insecticides of the future. The ability to develop resistance to insecticides is not shared equally

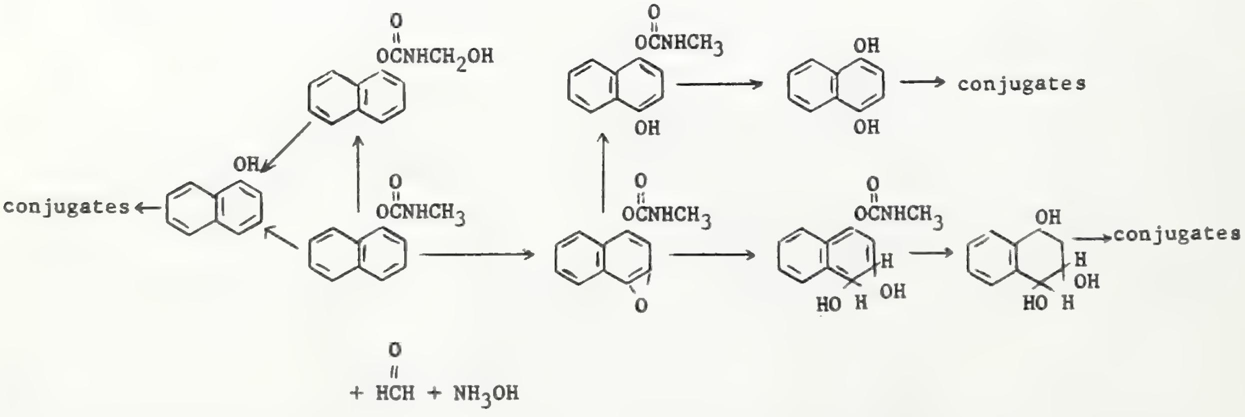


Figure 2.--Metabolic pathways of carbaryl (Sevin) in insects and vertebrates.

by all insects. For example, the muscoid flies *Phormia regina*, *Callitroga macellaria*, and *Muscina stabulans*, although they frequent the same environment as the house fly, have not developed any appreciable resistance to DDT, under conditions where the house fly rapidly developed total immunity (3).

Strains of insects highly resistant to one insecticide seldom, if ever, are tolerant to a wide variety of pesticides. This is graphically shown by the data in table 9, where the toxicity of a number of insecticides is compared to a fully susceptible S_{NAIDM}, a DDT- and cyclodiene-resistant strain R_{SP}, and a malathion- and Chlorthion-resistant strain R_{SC}. It is evident that strains of flies totally immune to a given insecticide remain fully susceptible to compounds with differing modes of action (compare DDT and trimethyltin chloride). More importantly, minor structural changes, such as the addition of a single *o*-chlorine to DDT, almost completely overcome the DDT resistance by blocking the dehydrochlorination of the compound by the detoxifying enzyme DDT'ase (27). Similarly α-deutero-DDT has been proposed as a remedial insecticide for DDT-resistant *Aedes aegypti*, the carbon-deuterium bond proving less susceptible to enzymatic action than the carbon-hydrogen bond of DDT (34). Although the carbamate *o*-isopropylphenyl *N*-methylcarbamate is highly toxic to susceptible house flies, it was completely ineffective against the resistant strains selected by DDT and the cyclodienes and by malathion and Chlorthion (table 9). However, the closely related *m*-propargyloxyphenyl *N*-methylcarbamate was toxic to all three strains and the thiolane oxime *N*-methylcarbamate showed no

Table 9.--Comparative toxicity of some insecticides to susceptible and resistant house flies[1]

Insecticide	Topical LD_{50} μg. per ♀ fly		
	S_{NAIDM}	R_{SP}	R_{SC}
DDT	0.04	>100	>100
DDT + 0.2 pt. *N*,*N*-dibutyl-*p*-chlorobenzenesulfonamide	.03	3.2	2.4
(*o*-Cl-DT) 2-(4-chlorophenyl)-2-(2,4=dichlorophenyl)-1,1,1-trichloroethane	.22	.72	.43
Dieldrin	.02	>100	>100
Malathion	.54	2.1	>100
Chlorthion	.23	.22	>100
O-ethyl *O*-2,4,5-trichlorophenyl *N*-ethylphosphoramidothioate	.09	.17	.16
Trimethyltin chloride	1.1	1.6	1.6
o-Isopropoxyphenyl *N*-methylcarbamate	.47	>100	>100
o-Isopropoxyphenyl *N*-methylcarbamate + 5 pt. piperonyl butoxide	.14	.44	.39
m-Propargyloxyphenyl *N*-methylcarbamate	.15	.72	.38
1,3-Dithiolane-2-oxime *N*-methylcarbamate	.022	.024	.025

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[1] Metcalf, R.L., unpublished data.

signs of cross tolerance to either resistant strain.

An informative example of the effects of small changes in chemical structure on resistance and the detoxifying enzymes is the toxicity of malathion to susceptible and resistant *Culex tarsalis* mosquito larvae (table 10). Matsumura and Brown (19) have shown that malathion resistance, which is due to a single partially dominant gene allele, is (like malathion resistance in the mammal, fig. 1) largely the result of increased carboxyesterase. This enzyme in *Culex tarsalis* is also susceptible to inhibition by EPN, which acts as a synergist for malathion against the resistant strain. The malathion resistance could be completely reversed by changing the ester group from ethyl, as in malathion, to methyl, as shown in table 10. These data demonstrate the high specificity of the carboxyesterase detoxication enzyme, which has a concentration in resistant larvae of about 13 times that in susceptible larvae (20).

Synergists, such as EPN, that inhibit the action of the detoxication enzyme may be used to restore the susceptibility of the resistant species. *N*,*N*-dibutyl-*p*-chlorobenzenesulfonamide ("Anti-Resistant") is a strong inhibitor of DDT dehydrochlorinase and, as shown in table 9, substantially restores the action of DDT to resistant house flies. The hydroxylation detoxication mechanism of carbamates, previously discussed (fig. 2), is a critical factor in determining house fly resistance to these insecticides and can be developed to high levels by continued selection (10). This enzyme is inhibited by piperonyl butoxide and other methylenedioxyphenyl compounds, and these effectively synergize carbamates against resistant house flies (table 10).

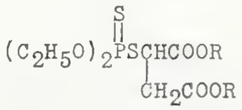
ENVIRONMENTAL CONTAMINATION AND ECOLOGICAL MAGNIFICATION

Perhaps the area of greatest concern in the present-day use of pesticides is the extreme persistence of the widely used chlorinated organics, such as DDT and dieldrin, and their accumulation and storage in animal lipids. DDT is virtually omnipresent in human fat, averaging in parts per million 3 to 7 in the United States, 0.8 in Eskimos, 2.3 in meat abstainers, 140 in pesticide applicators, and reaching 648 in a worker in a DDT-formulating plant. Although no ill effects have been associated with any of these levels of DDT storage, its ubiquitous presence is clearly undesirable. Fortunately DDT in human fat has a well-defined biological half-life and is slowly metabolized and excreted in the urine, principally as DDA (4,4'-dichlorodiphenylacetic acid). As a consequence, careful studies by the U.S. Public Health Service have shown no increase in DDT-storage rates in the U.S. population since 1950: Average values in parts per million in 1950 - 5.3, 1955 - 7.4, 1954-56 - 4.9, 1961-62 - 3.9 (11).

The more serious aspect of this lipoid solubility and biological stability of DDT and related compounds is the biological magnification of in vivo storage, which may take place

Table 10.--Toxicity of malathion analogs to susceptible and resistant mosquitoes (*Culex tarsalis*) (5)

[LC 50 p.p.m.]

 $(C_2H_5O)_2\overset{S}{\overset{\parallel}{P}}S\underset{CH_2COOR}{\underset{\mid}{C}}HCOOR$	Susceptible	Resistant	Ratio R/S
CH_3....................	0.12	0.13	1.0
C_2H_5....................	.025	1.5	60.0
C_3H_7....................	.09	3.1	34.4
iso-C_3H_7..................	.19	.86	4.5

when these materials enter food chains. A classical example illustrating this problem relates to the use of TDE or DDD (2,2-bis(p-chlorophenyl)-1,1-dichloroethane) to control the Clear Lake gnat (Chaoborus astictopus). This nonbiting gnat is an important pest in a resort area because of its incredible abundance. Herms recorded that 85 million adult gnats weighing about 85 pounds were caught in a single night at one light trap. TDE was chosen for application to the 41,600-acre lake because of its high toxicity to the gnat larvae and relative safety to fish. The entire lake was treated with TDE at 14 p.p.b. in 1949, using 14,000 gallons of 30-percent emulsifiable concentrate. This resulted in spectacular control, and no gnat larvae were found for nearly 2 years until reinfestation occurred from neighboring lakes. Re-treatments in 1954 and 1957 were equally successful. However, adverse effects were subsequently noticed in the populations of such carnivorous birds as the Western grebe and the California gull. Analytical studies of the food chains in Clear Lake showed that 2 years after treatment plankton contained 5.3 p.p.m. of TDE, although no insecticide could be found in the water. Plant-eating fish contained from 40 to 300 p.p.m. of TDE and carnivorous fish, such as the brown bull head, 2,500 p.p.m. The Western grebe and the California gull feeding on these fish contained 1,600 to 2,000 p.p.m. of TDE (13).

The problem at Clear Lake has been solved to the satisfaction of both conservationists and property owners by the substitution of methyl parathion (0,0-dimethyl 0-p-nitrophenyl phosphorothioate) as a larvicide. This insecticide has an LC_{50} value to first-instar gnat larvae of 1.2 p.p.b. compared with an LC_{50} of 115 p.p.b. for the most susceptible fish present, the bluegill sunfish (Lepomis macrochirus). Methyl parathion is readily hydrolyzed in animal tissues and excreted as p-nitrophenol conjugates and phosphoric acid esters and thus does not accumulate in food-chain organisms. In 1962, three applications over a 2-month period at 2.3 to 3.3 p.p.b. gave acceptable gnat control and have provided a new concept of repeated low-level applications to kill the immature larvae. No adverse effects on wildlife have been demonstrated (12).

The problems of environmental stability and biological magnification of pesticide residues demand extensive study. In many cases, the highly stable chlorinated organics can be replaced by esters, such as the organophosphates and carbamates. Malathion and carbaryl (Sevin, or 1-naphthyl N-methylcarbamate) have generally wide margins of selectivity and are rapidly degraded and excreted as water-soluble metabolites, so that there is no appreciable storage in animal fats. The metabolic pathways of excretion of malathion have been illustrated previously (fig. 1). Carbaryl is believed to be detoxified, essentially as shown in fig. 2 (6).

Although carbaryl is normally effective for insect control from 5 to 15 days, its half-life in water and soil is of the order of 1 week. Significant residues in animal tissues do not persist for more than 1 week. No contamination of cow's milk has been observed within the level of existing analytical methods. Thus, the use of this compound represents an important step forward in ameliorating the problem of environmental contamination (1).

Despite the usefulness of malathion, carbaryl, and other newer esters as replacements for the very stable DDT and cyclodiene insecticides, there is real need for persistent insecticides of this type to control many insect pests of forests, field and forage crops, rangelands, and of man and animals. Methoxychlor (2,2-bis(p-methoxyphenyl)-1,1,1-trichloroethane), a pesticide closely related to DDT, is much more selective than the latter, with an oral LD_{50} to the rat of 6,000 mg. per kilogram as compared with 250 for DDT. It has a high degree of insectidical activity, as shown in table 1. Most important, methoxychlor is much more rapidly eliminated from the animal body and thus is free from the major problem of fat storage and presumably of ecological multiplication. The data in table 11 contrast the behavior of DDT and methoxychlor when fed to rats.

The methoxychlor residues stored after feeding at 500 p.p.m. declined very rapidly and could not be detected 2 weeks after cessation of feeding.

A recent study with human volunteers fed for 8 weeks with methoxychlor at 2 mg. per kilogram of body weight per day and supported by extensive clinical and histological studies has shown the safety of methoxychlor at 200 times the maximum permissible dietary level (39).

Table 11.--DDT and methoxychlor residues stored after feeding rats for different periods and at various rates[1] (16, 17)

Insecticide and weeks fed	Amount fed	Residues stored in--	
		Males	Females
	P.p.m.	P.p.m.	P.p.m.
DDT, 15....................	1	13	18
	50	284	588
Methoxychlor:			
18....................	25	0	
	100	1	
4....................	500	36	17

[1] Storage at 10-20x intake for DDT and 0.01-0.1x intake for methoxychlor.

Methoxychlor has been known since 1944. Despite its safety, high official tolerances on agricultural commodities (up to 100 p.p.m. as compared with 7 p.p.m. for DDT), and potential freedom from the problems of environmental contamination, it has had only limited usage. Annual consumption in the United States is estimated at less than 5 million pounds as compared with 70 million pounds for DDT. The U.S. Department of Agriculture Agriculture Handbook 120, "Insecticide Recommendations" 1961, lists only 81 uses for methoxychlor as compared with 334 for DDT. Although the lower overall insecticidal effectiveness and more particularly the higher price (about $1 per pound as compared with $0.20 for DDT) may explain methoxychlor's relative unpopularity, it is evident that methoxychlor should be the preferred material in any application where storage in animal tissues is a factor. This has in fact been achieved only in the case of direct applications to livestock and applications to alfalfa and other hay crops intended for dairy cattle feed, where it has been shown that methoxychlor is not excreted in milk.

In conclusion, it seems clear that the chemist and toxicologist are capable of tailoring insecticidal molecules, incorporating almost any combination of desirably selective properties. However, there remains the equally important problem of insuring that these superior molecules replace less desirable compounds in practical pest control. This can be encouraged best through appreciation of the biochemical and ecological dimensions of the living environment into which the pesticide is projected and by widespread utilization of the principles of integrated pest control. This symposium is a significant step in bringing us closer to this goal.

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CHARACTERISTICS AND REQUIREMENTS OF HERBICIDES FOR THE FUTURE

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The human, domestic animal, and wildlife populations of the world today cannot exist in the original environment of the past. Man's survival is directly dependent on the efficiency and safety with which he changes his environment and adjusts to it.

One of the irreversible changes man must make in his environment is the ecological shift from the natural climax vegetation to one that is satisfactory for the production of food, fiber, and forage crops, which are the products of his creativity. Too often this highly significant and essential change in man's environment is taken for granted. Far too few of us realize that the native vegetation in most areas of the world was not very efficient or economical as a source of food.

The plant successions that occur when native vegetation is disturbed or when cultivated fields are abandoned are well known. Weeds comprise an early stage of plant successions that terminate with the climax vegetation characteristic of an area. This ecological principle establishes the need for efficient weed- and pest-control technology. The control of weeds is basically an ecological problem (fig. 1).

The world need for food and fiber requires utilization of all available scientific technology to produce and protect high value food, forage, and fiber crops. Weed control is an essential part of this fundamental ecological process (5).

Weeds compete for water, mineral nutrients, light, space, and other growth requirements.

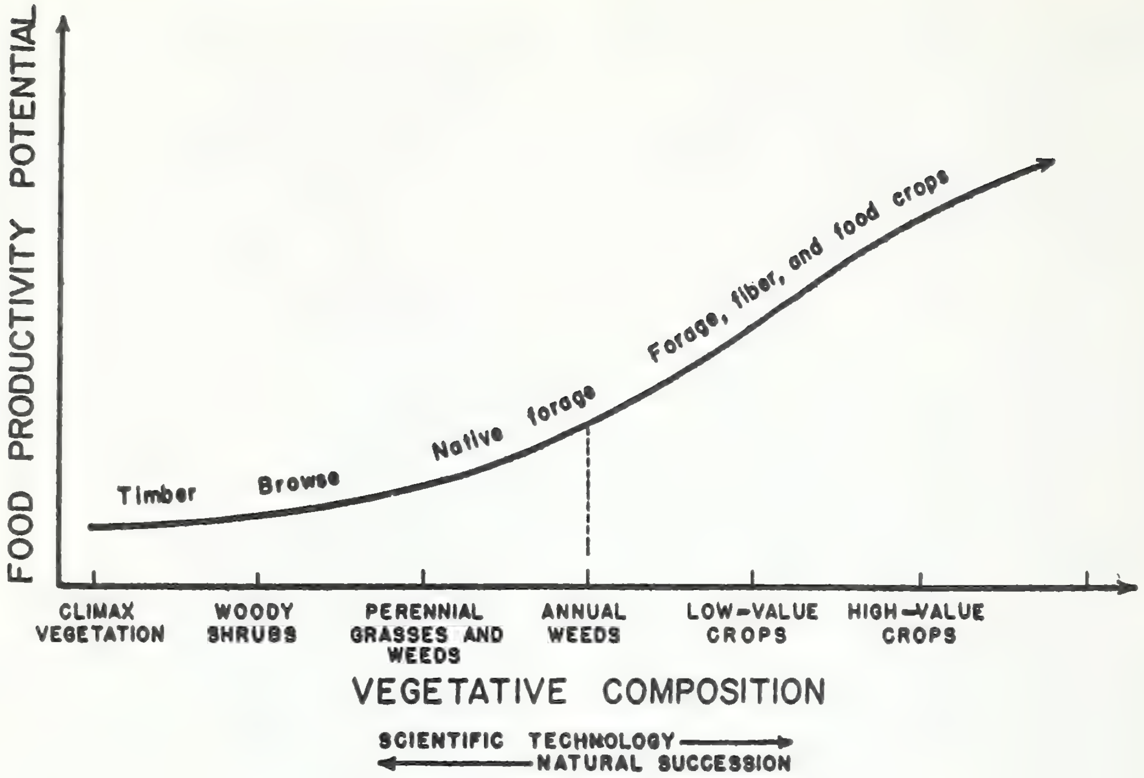


Figure 1.--(From Shaw et al. (6).)

These are the active ingredients of man's existence and survival. Weeds damage the total economy.

The annual losses due to weeds are about $2-1/2 billion. In addition, farmers spend about $2-1/2 billion each year to control weeds. Thus, the losses due to weeds and the cost of their control in the United States are estimated to exceed $5 billion each year (7).

Scientists have accepted the weed challenge, and they have turned weed science into a revolution, which has advanced through a succession of control techniques and methods that involve the use of energy of man and livestock, as well as mechanical devices ranging from the sickle to the diesel tractor. But laborious methods of hand weed control, such as the hoe and machete, have remained with us in many parts of the world as obstacles to the efficient mechanization of crop production.

One of the most important objectives of research and of regulatory and educational programs is the reduction of weed losses and the cost of their control by effective methods that do not injure man, animals, plants, soil, forests, fish, or wildlife. Through science and technology, chemicals have been developed to replace physical energy for weed control. This development has opened new horizons for increasing the efficiency of American agriculture. This significant advance has also created some problems that will require a constant review of research and educational programs (1).

The purpose of this paper is to review some of the requirements of chemical weed control of the future as a primary method and in combination with ecological, cultural, mechanical, biological, and other methods.

SCOPE AND USE OF CHEMICAL-CULTURAL WEED-CONTROL METHODS

The weed-control operations in the United States almost defy imagination. Cultural, mechanical, ecological, and other biological methods of weed control are used on 365 million acres of intertilled and drill-seeded cultivated crops each year. The intertilled row crops receive two to five seedbed tillage operations and an average of about five cultivations each year. In addition, nonchemical methods of weed control are used on a high percentage of the more than 1 billion acres of forage and grazing land. Weeds are also controlled on millions of acres of noncrop land each year.

Seedbed preparation, cultivation, and weed control require the use of 4-1/2 million farm tractors that supply 120 million horsepower in moving more than 250 billion tons of soil each year. This amount of soil would make a ridge 100 feet high and 1 mile wide from New York to San Francisco. This is the largest materials-handling operation in the world and the costs are enormous. About one-half of this operation is practiced solely for the control of weeds (3).

In 1962, cultural and other biological or nonchemical methods of weed control were used on about 75 percent of the national crop acreage. Chemical methods, combined with cultural practices, were used on about 25 percent (8, 9). Herbicides were used on more than 70 million acres of agricultural land in 1962 at a cost of more than $272 million, as compared with 53 million acres treated in 1959 at a cost of almost $128 million (table 1). This amounted to a 33-percent increase in the acreage treated with herbicides in the 4-year period. Expenditures for herbicides increased 112 percent during the same period.

Not only has the acreage treated with herbicides increased each year, but a greater diversity of herbicides is available today than ever before. In 1944, for example, there were only about 14 herbicides; in 1964, farmers had a choice of about 125 basic herbicides available in about 8,000 registered products.

The widescale use of herbicides during the past 20 years, their advantages and disadvantages, progress made in weed control by their use, and problems evolved during this period provide a partial basis for considering the characteristics needed in herbicides of the future.

CHARACTERISTICS OF HERBICIDES IN THE FUTURE

The characteristics of herbicides in the future will be determined by the chemical

Table 1.--Comparison of estimated extent and costs of chemical weed control in United States, 1959 and 1962[1]

Crop or area	States Reporting		Total area treated		Harvested acreage treated		Total cost of all herbicides and applications		Average cost per acre of all treatments			Acreage treated by--			
												Farmers		Custom operators	
	1959	1962	1959	1962	1959	1962	1959	1962	1959	1962	Change	1959	1962	1959	1962
	Number	Number	1,000 acres	1,000 acres	Percent	Percent	$1,000	$1,000	Dollars	Dollars	Percent	Percent	Percent	Percent	Percent
Corn	40	46	20,051	25,302	24.5	38.8	37,980	57,600	1.89	2.28	20.6	82	83	18	17
Cotton	13	15	1,554	5,433	10.3	34.9	4,628	16,805	2.98	3.00	3.7	92	91	8	9
Soybeans	15	28	556	2,827	2.5	10.2	2,315	10,835	4.16	3.83	-7.9	98	90	2	10
Small grains	38	45	20,723	18,931	21.6	23.5	37,095	29,579	1.79	1.56	-12.8	75	65	25	35
Rice	4	6	502	940	31.7	53.0	888	6,250	1.77	6.65	275.7	13	66	87	34
Peanuts	5	8	35	320	2.4	22.0	116	2,565	3.33	8.27	149.8	100	97	(2)	3
Sugarbeets	11	15	125	362	13.8	32.8	625	2,237	5.05	6.18	23.6	94	65	6	35
Sorghum	14	25	2,093	2,665	13.6	23.1	6,512	5,258	3.11	1.97	-36.7	40	65	60	34
Forage seeds	14	20	282	439	7.8	16.0	1,868	2,416	6.62	5.50	-16.9	80	62	20	33
Vegetables	20	29	276	951	9.9	35.5	1,418	8,634	5.14	9.09	76.7	84	75	16	25
Potatoes	--	4	--	171	--	12.3	--	1,017	--	5.95	--	--	100	--	0
Dry beans	--	2	--	16	--	1.1	--	114	--	7.12	--	--	95	--	5
Sweet corn	--	1	--	30	--	4.6	--	187	--	6.23	--	--	95	--	5
Onions	--	1	--	26	--	27.0	--	650	--	25.00	--	--	98	--	2
Fruits and nuts	9	21	[illegible]	[illegible]	[illegible]	9.7	43	2,397	8.60	8.98	4.4	99	86	1	14
Strawberries	3	--	[illegible]	--	[illegible]	--	55	--	11.20	--	--	97	--	3	--
Ornamentals	6	15	[illegible]	[illegible]	1.0	24.8	45	969	22.50	19.00	-15.6	70	34	30	[illegible]
Hay	20	33	[illegible]	[illegible]	.4	0.6	1,692	3,580	6.22	8.69	39.7	81	78	19	[illegible]
Subtotal	--	--	[illegible]	59,133	14.8	20.8	[illegible]	151,093	2.05	[illegible]	24.9	--	--	--	--
Lawns	17	22	60	672	.8	8.4	1,489	15,368	24.82	22.86	-7.9	82	83	18	17
Pastures	34	45	2,400	4,714	.8	1.5	5,789	13,340	2.41	2.83	17.4	74	64	26	36
Rangeland	13	20	2,011	2,262	.3	.4	6,174	6,265	3.07	2.77	-9.8	37	37	63	[illegible]
Forest plantings	--	18	--	274	--	--	--	2,752	--	10.04	--	--	--	--	--
Noncropland	27	31	1,971	3,612	--	--	19,738	83,714	10.01	23.18	131.6	30	34	[illegible]	[illegible]
Subtotal	--	--	6,442	11,534	[3] .5	[3] 0.8	33,190	121,439	5.15	10.53	104.5	--	--	--	--
Grand total	41	50	52,923	70,667	[3] 4.0	[3] 5.4	128,471	272,532	2.43	3.86	58.8	--	--	--	--

[1] Data summarized from reference 9.

[2] Less than 0.5 percent.

[3] Excludes treated acreage of forest plantings and noncropland.

weed-control needs of the future and the integration of chemical and nonchemical methods in crop, range, and forest production and the utilization of water resources and noncrop land areas.

Trends since 1944 strongly suggest that the use of herbicides will continue to expand at an equal or more rapid rate in the future (4, 5, 8, 9). All available survey data, as well as the requirements for efficient mechanized crop production, strongly indicate a continued expansion of herbicide usage.

Because herbicides are used to kill plants classified as pests, they are also appropriately called pesticides. Herbicides are, however, more than pesticides or protectants. They are crop-production chemicals, which reduce the man-hour, machine-hour, and machine-horsepower requirements of crop production. Their effects on other crop-production practices are also far reaching.

New chemical methods of weed control will affect choice of crop and variety; seedbed preparation; method of seeding; seeding rates; row spacing; plant spacing in the row; plant population; fertilization practices including type, time of application, and placement; cultivation; irrigation practices; harvesting; seed-cleaning operations; erosion control; fallow practices for weed control; disease- and insect-control practices; pasture renovation; pasture and range management; clearing new lands for crops or pasture; forest management; utilization of farm water resources for irrigation and recreation; and maintenance of reservoirs, drainage ditches, ditchbanks; irrigation canals, and arm roadsides.

Increased specificity and selectivity will be essential requirements of herbicides in the future. Highly specific herbicides will be used to control specific weeds in specific crops and on noncrop lands utilized for specialized purposes. There will also be increasing demands for broad-spectrum herbicides for the control of diverse weed populations but without broad-spectrum toxicity to crops and nontarget organisms in the total environment.

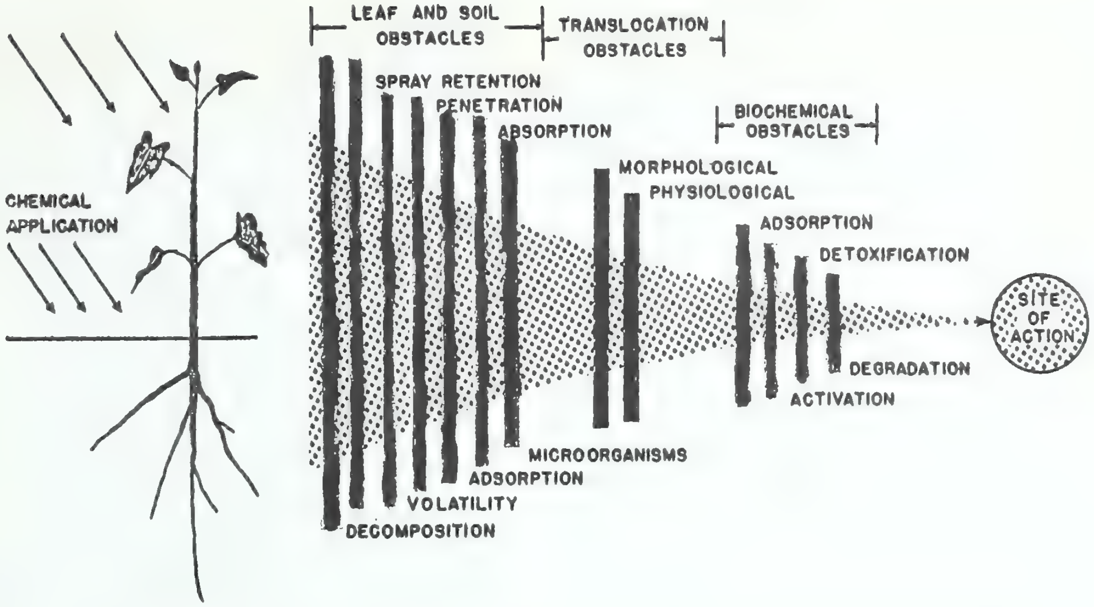
The fundamental requirements for future expanded use of herbicides without harmful effects in man's total environment can and must be accomplished.

BASIC RESEARCH IS KEY TO FUTURE HERBICIDE REQUIREMENTS

In order to achieve the requirements for herbicides in the future, our fundamental knowledge of the relation between molecular structure and herbicidal activity must be expanded. A better understanding of the penetration, absorption, and translocation of herbicides in plants must be developed. The mechanisms of phytotoxicity and selective action must be more fully determined. The fate of herbicides in plants and soils and our total environment must be more fully understood, including primary, secondary, and cumulative effects on nontarget organisms (2, 6; fig. 2).

The results of the total weed science research effort in meeting the present requirements for herbicides provide a basis for optimism that the herbicide requirements of the future can also be attained (2). A few selected examples will illustrate some of the principles that will need extension in the future. The use of surfactants, cosolvents, carriers, and other formulation ingredients, based on knowledge of the entrance and movement of herbicides in plants and their persistence, will reduce herbicide rates of application, decrease or increase persistence, lower the cost of application, and prevent or minimize residues in plants and soils. Such knowledge also permits use of low or nontoxic ingredients to reduce the amounts of higher toxicity ingredients in the formulation. The development of the 3-(3,4-dichlorophenyl)-1, 1-dimenthylurea (diuron)-surfactant treatment, as a directed postemergence application for weed control in cotton, is an excellent example of utilizing this principle in developing a widely used, safe, and effective practice.

Research on the mechanisms of action of herbicides has revealed that plants differ in their capacity to metabolize herbicides and that this property is highly specific. The conversion of a nonphytotoxic chemical, 4-(2,4-dichlorophenoxy) butyric acid (2,4-DB), to the highly effective herbicide, 2,4-dichlorophenoxyacetic acid (2,4-D), by some weeds while certain crops do not cause this conversion provides a highly selective mechanism of



OBSTACLES THAT DETERMINE CONCENTRATION OF TOXIC MATERIAL AT SITE OF ACTION

Figure 2.--(From Shaw et al. (6).)

chemical weed control. In some instances, plants detoxify herbicides to inactive forms. The conversion of 2-chloro-4,6-bis (ethylamino)-s-triazine (simazine) to a nonphytotoxic form in corn, but not in many weeds and other crop plants, is a classic example of herbicide selectivity dependent on differential metabolism of herbicides in plants. These are examples of widely effective herbicides in controlling weed populations but with high tolerance and selectivity of action on a few crops with few if any harmful effects. These contrast sharply with such a herbicide as pentachlorophenol (PCP), which has high toxicity to nontarget organisms in the environment. The current trend is clearly toward compounds with greater specificity and selectivity and low toxicity to nontarget organisms.

NEW APPROACHES IN DEVELOPMENT OF HERBICIDES

In developing herbicides, more attention will be given to acquiring a better understanding of the life-cycle weaknesses in the growth of plants. Research emphasis will again be required. Chemicals are needed to stimulate the uniform germination of weed seeds at varying depths in the soil in a relatively short period of the growing season. This would permit their control with a single application of a nonpersistent herbicide. There is also a need for chemical inhibitors to induce long periods of weed-seed dormancy. This practice would cause a loss of viability in the seeds of many weeds resulting in their control. Chemicals to induce or break bud dormancy of perennial weeds could be used to stimulate growth in winter. Such effects might result in control by winterkill or in an increase in the susceptibility of perennial weeds to control by present herbicides and cultural methods.

Chemicals that prevent fertilization in weeds and weed-seed production need further consideration. These are but a few examples of approaches that may be explored in the future. Nevertheless, emphasis in all approaches will be on the development of herbicides that control weeds through mechanisms found in plants but not in animals and man and that are harmless to man and all other nontarget organisms in the total environment.

Not only will fundamental chemical and biological information be required, but it will be essential in shaping engineering objectives in weed control in the future. The types of equipment needed will undergo significant changes and the need for engineering research will greatly increase. Chemical weed-control equipment of the future will have unusual precision application requirements. The appropriate herbicide will be applied in the minimum effective amounts, at the most effective time, and precisely on the target.

In order to assure that herbicides of the future and their use patterns possess the desired characteristics, a multidiscipline and interdiscipline research and education approach will be required. Obviously the cooperative efforts of State, Federal, and industrial scientists and their interacting efficiencies in working together as a team in a well-balanced and effectively coordinated research program will be needed.

The use of herbicides, in some instances, is beginning to exceed the research information available to insure their safe use. If a better balance between research and herbicide use is not obtained and maintained in the future, the risk of damage to crops and man's total environment will increase. If a balanced research and education program is maintained, the problems of the future will not be beyond solution and will not involve undue risks.

The future of weed control will certainly be characterized by the discovery, development, and utilization of more efficient forms of energy. The versatility and effectiveness of herbicides for controlling weeds offer almost unlimited possibilities for improving the efficiency of weed control, but they are more effective when combined with other efficient nonchemical methods of control. Thus it seems that future progress will be largely determined by (a) discovery of more selective, more specific, better translocated, more efficient, better formulated, safer, and more economical herbicides; (b) understanding the effects of chemicals on plant growth, soils, and the total environment of man, domestic animals, and wildlife; (c) ingenuity in modifying and combining chemical and cultural practices; (d) understanding the limitations of current practices; (e) development of new and more effective techniques; and (f) discovery of more efficient sources of energy for selective weed control.

The rapid advance of weed-control technology and the acceptance of chemical weed-control practices by farmers are having, and will continue to have, profound effects on crop production and on soil and water management practices. Significant changes will necessitate a constant review of agricultural research and education objectives and direction.

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THE ROLE OF CHEMICALS FOR THE CONTROL OF VERTEBRATE PESTS

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Toxic substances have a long history of use by mankind as a means of capturing wild animals for food. Primitive peoples in South America and Southeast Asia applied mashed cube or derris root, which contains rotenone, to fresh and salt waters to stun and kill fish. Similarly Malaysian tribes used the derris root as an ingredient of arrow poisons (Leonard, 1939). The early Chinese used "fishing plants," particularly "tea-seed cake" made from the saponin-bearing seeds of camellia, to kill fish in ponds (Tang, 1961). The use of walnut hulls to immobilize and capture fish has also had a long history (Westfall et al., 1961).

TERRESTRIAL VERTEBRATES

It was a short step for man to extend his use of naturally occurring toxic materials to the destruction of animals that interfered with his interests. The early use of toxicants is evidenced by ancient Egyptian hieroglyphics depicting a bulb of the red squill plant alongside a dead rat. The drawing suggests that the rodenticidal properties of squill were known thousands of years ago. The toxic nature of strychnine was known to the Old World during the 1600's. According to one early writer, "The chiefest use that they are put unto is to kill Dogs and Cats, and other creatures by mixing some of it with meat, as also to give unto Crowes, Ravens, and other such-like troublesome birds that by their noyse disquiet mans sleepe or studies" (Young and Goldman, 1944, p. 323). Numerous other historical accounts lead one to suspect that our knowledge concerning the lethal properties of arsenic and strychnine is in part due to their use to eliminate individuals of another species of vertebrate, Homo sapiens.

Although circumstances surrounding the origin of some economic poisons are obscure, it appears that man's early knowledge of toxic substances was largely limited to a few botanicals and naturally occurring minerals. The fact that they were found to be lethal to one species of animal provided the clue that they might also produce similar effects on other creatures. Through trial and error by individuals confronted with animal pest problems, their use was spread to more and more species. This is illustrated by the early history of strychnine for the control of terrestrial vertebrates in North America. It was widely used by early settlers to destroy gray wolves that preyed upon their livestock. Large amounts were also employed by trappers to facilitate the collection of furbearers for their pelts.

According to Young and Goldman (1944), sometime about 1848 a shipment of strychnine was consigned from Philadelphia to a South American port, but news of the gold discoveries in California reached the vessel and the cargo was landed at San Francisco. The strychnine was sold there and used for the control of harmful animals. By the turn of the century it was applied extensively throughout the West for the control of predatory animals, rabbits, field and commensal rodents, and nuisance birds.

In 1912, the Bureau of Biological Survey initiated a program for the control of ground squirrels in national forests in California. During 1915, this activity was expanded to include predatory animals. The first Government laboratory to conduct research on lethal agents for the control of wild vertebrates was established at Albuquerque, N. Mex., in 1920 and moved to Denver in 1922. This laboratory was the predecessor of the present Denver Wildlife Research Center of the Bureau of Sport Fisheries and Wildlife. During the intervening years up to the present, the major part of the research on methods for controlling damage by wildlife has been carried out at that location. One of the laboratory's first accomplishments was the development of a scent containing oil of catnip as an attractant for trapping feline predatory animals. Now, some 40 years later, chemical attractants are still being sought as helpful tools for many types of pest control.

During the early 1900's, strychnine was supplemented by other vertebrate poison-bait formulations containing phosphorus, arsenic, mercury, and barium carbonate; two burrow fumigants, carbon bisulfide, and calcium cyanide were also in common use. In the 1930's, these were augmented by thallium sulfate, red squill, and zinc phosphide. A shortage of rodenticides during World War II set the stage for the discovery and development of numerous synthetic pesticides, including antu (alphanaphthyl thiourea), sodium mono fluoroacetate (1080), and the anticoagulant rodenticides (warfarin, pival, fumarin, etc.).

Several nonlethal chemical formulations for alleviating animal damage were developed during the latter period. These include a variety of rodent, rabbit, dog, cat, and deer repellants, as well as several bird deterrents. Aside from explosive gases used in mechanical scare devices, the repellent properties of these chemicals are based on objectionable taste or odor, unnatural color, or skin-irritation characteristics.

In more recent years the spectrum of research has been further broadened, and current screening programs encompass a search for compounds that produce numerous types of biological activities, including systemic chemicals to alter the palatability of plants as wildlife foods, either as repellents or attractants. The research also includes studies of chemosterilants and stupefactants.

AQUATIC VERTEBRATES

About 50 years ago, the need to control undesirable fish in sport fishery waters began to be recognized. The needs defined by Smith (1950) are to rehabilitate habitats for more desirable species either by destroying entire fish populations or by selectively removing undesirable species, to control diseases and parasites by killing fish that are disease carriers in hatchery water supplies, and to generally or selectively destroy diseased or parasitized populations in natural waters. Prevost (1960) stated that the rehabilitation of waters by poisoning fish is the best available tool. In a more recent and excellent summary, Hooper et al. (1964) concluded that the rehabilitation of trout lakes is sound management where fishing pressure is moderate to heavy and chances of contamination are low. They added, however, that more research is necessary before the total reclamation of warm waters will give predictable results.

Copper sulfate was the first material used in sport fishery management. Titcomb (1914) employed it to reclaim lakes, and although the chemical killed fish food organisms and aquatic plants as well as fish, it continued in small-scale use until derris root (rotenone) was introduced in 1934 (more than a thousand years after its utility was known to primitive man). As a result of trials in Michigan and New Hampshire, derris rapidly gained favor as a tool for rehabilitating lakes and streams. By 1949, 34 States and Canadian Provinces were using it (Solman, 1950). Some disadvantages of the powdered derris root were overcome by using emulsifiable and synergized preparations. The search for better toxicants has continued, however, because rotenone is considered to be expensive and inefficient in some situations.

Cresol was introduced in 1941 as an agent for collecting fish (Embody et al., 1941). DDT was tested as a fish toxicant in lakes in 1947, but it was not considered as effective as rotenone. Calcium hypochlorite has had some use since 1947 in eradicating fish from domestic water supplies because of the ease of neutralizing it with sodium thiosulfate.

Toxaphene became competitive with rotenone in 1948 because of its extreme toxicity to fish and its economy. Its hazards to other life and long persistence in water, however, caused the Bureau of Sport Fisheries and Wildlife and several States to discontinue its further use in 1963. Endrin was tested on fish in 1952 and was first applied as a general toxicant in lakes in 1958. Some successful applications were made in Asia against trash fish, and Sreenivasan and Natarajan (1962) concluded that it is the most powerful fish toxicant known. However, because of its high toxicity to other vertebrates, long persistence, and tendency to concentrate in tissues of higher animals, this chemical is not satisfactory for use in fish control.

Jackson (1956) demonstrated that pellets of sodium hydroxide dropped in the nests of sunfish would kill eggs and fry. In 1958, Bridges reported on the efficacy of sodium cyanide as a fish poison. It is toxic to fish at low concentrations, persists only a short time in water, and first anesthetizes fish before killing them. Fish may survive if removed promptly to fresh water. The compound, however, is highly dangerous to humans. Also in 1958, Applegate et al. related the results of research to find selective toxicants for the larvae of sea lampreys. The development of TFM (3-trifluoromethyl-4-nitrophenol)as a selective larvicide was a long step toward the control of sea lampreys in the Great Lakes by the United States and Canada (Applegate et al., 1961). It also stimulated increasing investigation to find and develop better general and selective toxicants for fish.

Saponin, a glucoside extracted from plants, was tested by Tang (1961) in Taiwan as a selective control for predaceous fish in intensively cultured shrimp ponds. Fish were successfully eliminated, but more work is needed to determine the effects of saponin on the food and the growth of shrimp. A malathion-dibrom mixture was introduced with some success in 1962 as a relatively selective control for certain sunfishes (Grice, 1962). In step with the times, investigations by MacPhee (1963) center on the specific toxicants for fish sperm and ova.

In 1963, Derse and Strong reported on the toxicity of antimycin to fish and indicated its promise as a fishery tool. Subsequently, research at the Fish Control Laboratories at LaCrosse, Wis., and Warm Springs, Ga., has been centered on this antibiotic product of Streptomyces. It appears effective against a wide variety of fish species and sizes, eggs to adults, in very small concentrations. It is easily applied; there is little evidence of hazard to fish food organisms; it is effective over a wide range of temperatures; and it degrades rapidly in water (Walker, et al., 1964). The product is currently undergoing thorough testing in the laboratory and field.

In his critique of the need and use for fish poisons, Miller (1950) pointed out a general lack of follow-up studies or controlled experimentation with toxicants. He complained that the literature is limited on data on the completeness of kills, fish recovered, and rapidity of repopulation of undesirable species. There is also a dearth of information about the hazards involved. Until recently, the application of toxicants for fishery management often preceded research on their side effects. This situation, fortunately, is now being remedied through the efforts of formal investigations on chemicals as tools in fishery management (Hooper et al., 1964; Lennon and Walker, 1964).

FUTURE TRENDS

Increased public awareness of fish and wildlife values, both economic and esthetic, has resulted in considerable opposition to the continued use of broad-spectrum lethal agents for many kinds of pest control. As stated by Baldwin (1964), "There is a growing concern, coupled with positive action, for the preservation of all forms of plant and animal life." This recognition along with mounting public interest in the effects of toxic chemicals on human health are, in large measure, due to the widespread publicity concerning pesticides aroused by publication of the book "Silent Spring" in 1962 by the late Rachel Carson. The next year this was followed by a report on the "Use of Pesticides" by the President's Science Advisory Committee. The recommendations in this report have had a strong effect on numerous kinds of pesticidal research during the current year.

The future role of chemicals in the control of vertebrate pests will be increasingly dependent on new knowledge acquired through the combined efforts of chemists and biologists. Priority is being given to nonlethal chemical methods for the management of fish and wildlife populations. Although the work includes a continuing and expanding search for selective lethal agents, their utility will be contingent upon their degree of specificity for target species and nonpersistence in the environment.

Over the millions of years that multicelled organisms have been evolving, they have developed a fantastic capability within themselves to quickly synthesize complex chemical compounds, each having a special arrangement for one specific task. Among the vertebrates this internal "chemical factory," on challenge by a foreign antigen, can produce not one but literally tens of thousands of different antibodies, each of which is tailormade for one purpose. Our skills at chemical synthesis in the laboratory have nowhere near reached this degree of perfection. However, encouraging progress is being made toward finding chemical means of attacking certain commonly occurring enzymes (or chemical precursor systems), where the mechanism of action is understood well enough to permit adaptation to specific problems of vertebrate control. For example, the anticoagulants (-4-hydroxycoumarins and the -1-3-indandiones) interfere with the synthesis of prothrombin in the blood. They are the outgrowth of studies to discover the cause of "sweet clover disease," a hemorrhagic ailment in cattle. It was found that the cause of this disease was the anticoagulant dicoumarin. The initial objective of later work was to find more active anticoagulants to prevent post-operative blood clots in humans. Our present-day anticoagulant rodenticides are byproducts of this medical research.

Most of the major chemical and pharmaceutical companies conduct screening programs to discover new pesticides. The number of test organisms is necessarily limited to a few species. It is unusual to have the initial screening include more than one species of mammal, one species of bird, and one species of fish. Since the mammal is often an albino rat or mouse, we can expect to find that most "specific" rodenticides apply to this group.

In the search for an antiinflammatory drug, scientists at the McNeil Laboratories used mice as the test species. Having found several promising compounds that the mouse tolerated fairly well (nontoxic), the study was extended to include the white rat for confirmation of the anti-inflammatory effect. Much to everyone's surprise, the drug proved highly lethal to rats. Intensive work with this laboratory animal revealed that the drug Norbormide resulted in irreversible constriction of the blood vessels. So specific is the action of this drug on the enzyme system in the Norway rat that the closely related roof rat requires five times the quantity, whereas the house mouse is not affected until dosages of 2,500 mg. per kilogram are reached. Best of all, the beneficial species most likely to come into contact with baits placed for Norway rat control show no vasoconstriction from the drug. This list includes dogs, cats, sheep, hogs, cattle, chickens, ducks, turkeys, and some 15 other species. As might be expected, if the investigation is carried far enough with other species, a few show toxic response but at much higher levels than for the brown rat (rabbits, guinea pig, hamster, nutria).

Red squill and antu are also unique because of their high toxicity to the Norway rat and wide margin of safety for other animals. The specificity of squill is due to emetic effects of the toxic agent. Unlike most mammals, the rat cannot regurgitate. In the case of antu, its high degree of specificity is due to a wide differential in toxicity to various species and even within species. The LD_{50} to Norway rats is 8 mg. per kilogram, whereas the LD_{50} to roof rats is 220 mg. per kilogram.

These examples are but a few of the many kinds of selective effects that may be produced by different chemicals. Our knowledge of those that are highly specific for rats is in large part due to the extensive use of laboratory rats in medical research. Their discovery illustrates the importance of using target species in screening programs if we are to find substances for use in the management of vertebrate populations.

A start has been made during the past year to provide the chemical industry with guidelines for conducting tests of candidate pesticides on several indicator species of fishes, birds, and mammals. The tests are in addition to those routinely conducted to determine efficacy and safety to man and domestic animals. Data from these studies will provide early clues as to whether a new compound is likely to be hazardous to wildlife species other than target organisms. In some cases, the data may also reveal potential utility for other purposes.

A new avicide, known under the code designation DRC-1339, shows considerable promise as a slow-acting oral toxicant for use in starling control. It is 300 to 500 times more toxic to starlings than to rats, indicating a wide margin of safety for mammals. DRC-1339 illustrates another mode of action, in that it interferes with the oxygen-carrying capacity of hemoglobin and causes tissue suffocation or methemoglobinemia. Its higher toxicity to avian species is presumably due to their more rapid rate of metabolism in comparison to mammals. Our interest in the compound stemmed from industry data on its differential in toxicity to laboratory rats and domestic chickens. Although this avicide is highly toxic to a number of avian species, its hazard to them can be controlled. For example, the baiting of starlings at northern livestock feedlots is carried out during winter months after most other birds have completed their southern migration and prior to their return in the spring.

The present program for control of the lamprey in the Great Lakes illustrates chemical selectivity in an aquatic environment. More than 6,000 compounds were tested by the Bureau of Commercial Fisheries in its search for an effective material. The work resulted in discovery of the lampricide TFM (3-trifluoromethyl-4-nitrophenol). At levels of 1 to 17 p.p.m., depending on the chemistry of the water, it is highly lethal to lamprey larvae. These concentrations have little effect on most other forms of aquatic life in treated streams. The previously mentioned fish toxicant, antimycin, is another example of how selective control of certain species can be achieved in aquatic habitats.

Most of the vertebrate pesticides in use, including those recently developed, are toxic to vertebrates of many species, although the exact lethal dose may vary. They owe their usefulness to man's technical ability to devise safeguards for beneficial species occupying the same habitat. For example, by carefully controlling the concentration of strychnine in baits, a treated grain can be produced that will kill field mice and ground squirrels, but quail, pheasants, and domestic poultry can consume it without lethal effect. The mourning doves that might also feed on the grain are endangered by these rodent-control levels of strychnine. This problem is corrected by changing both the shape and color of the grain, to which change doves and many small seed-eating birds show an avoidance reaction. Similar devices of formulation, placement, and timing have evolved a margin of safety for beneficial species over the many years of strychnine use. Such techniques must rely on careful programing by the user, which is not always possible when control chemicals are placed in the hands of untrained or careless individuals. This margin of error, small as it may be, is the basis for much of the current concern about the hazards of broad-spectrum pesticides.

Competing forms of life take advantage of man's every step to increase the production of food and fiber. Through the many changes we have wrought, we can no longer rely on antiquated methods for protection from pests. Our need for chemical tools will grow. Selective lethal agents, chemosterilants, synthetic attractants, and systemic repellents now loom on the horizon. They exemplify the versatility of modern chemical technology. We must make greater use of that field of science in the development of better methods for pest control.

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THE FUTURE ROLE OF NATURAL AND SYNTHETIC ATTRACTANTS FOR PEST CONTROL

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Whether we agree with the late Rachel Carson or not, it is clear that this talented author found a weak point in our scientific armament and she dramatized the need in "Silent Spring" for research in the vital area of pesticides (1).

This statement is not meant to imply that our chemists, entomologists, public-health officials, and others responsible for synthesizing, testing, advocating, selling, or condoning the use of pesticides are at fault. On the contrary, these workers have put to excellent use our expanding knowledge of chemistry and biology. Their chemicals and techniques of employing chemicals have saved millions of lives. These efforts have been so effective that we have to cope with such immediate problems as what to do with our food surpluses and such long-term problems as the human population explosion.

Evolutionary processes being slow, who would have predicted that insects would have built up an immunity to our wonder chemicals in less than a decade? Species of insects resistant to insecticides can now be counted in the hundreds (2), and this problem is one of the biggest we face today. Increasing the amount of insecticide would only increase the threat of contaminating our food, our environment, and ourselves. Clearly, means are required to supplant or alleviate the need for toxic pest-control chemicals, and new approaches to the control of insect pests deserve to be investigated fully.

With this background, it is easy to see why the idea of using innocuous odors to control insect pests is particularly inviting these days.

Are we grabbing at straws, or does this approach really have substance? There is already enough well-documented evidence to establish the value of attractants in pest control. Before venturing off into the misty future, allow me to present some of this evidence.

Thus far attractants have proved useful for two purposes--detection of infestations and direct control. In either case, these techniques are based on the well-established fact that the survival of many insect species is fostered by their keen, specialized sense of smell, which guides them to food, the opposite sex, or a place to lay eggs (3). Social insects even manufacture their own odors, which they employ to warn others in the colony of impending danger, to recognize intruders, to gather food, or to enlist the aid of other colony members (4). The action of some of these odors is powerful enough in terms of the infinitesimal quantities needed and intensity of response to make them potentially valuable for combating economically important species. We would like to employ this important insect survival mechanism to control and even to eradicate harmful insects.

The powerful attractants found thus far are highly specific, that is, they will attract one or a few closely related species and then only the males.

For detection purposes, traps are baited with a specific lure; wherever insects are caught and as long as they are caught, control measures may be applied. This makes for a most efficient operation. Insecticides are not spread needlessly. Money is saved because insecticides are not wasted. Residues are held to a minimum.

The further spread of the gypsy moth [Porthetria dispar (L.)] from the Northeastern United States has been prevented for at least 20 years now through the use of traps baited with a stabilized sex attractant for the moth (5). Soon after the female gypsy moth emerges from pupation it emits an odor, i.e., a sex attractant, which lures the male to it for mating. The attractive odor ceases after mating. At first, traps were baited with a stabilized extract laboriously obtained at great expense from hundreds of thousands of virgin female moths. In 1960, the sex attractant was identified and synthesized (6), and subsequently a closely related attractant called gyplure was synthesized from the commercially available ricinoleyl alcohol (7). The comparatively inexpensive gyplure is now used to bait the 50,000 traps set out in the New England area every year to map the whereabouts of the moth.

When the highly destructive Mediterranean fruit fly [Ceratitis capitata (Weidemann)], or medfly, turned up in Florida in 1956, specific powerful attractants (8) in traps pinpointed the pockets of infestation and guided the application of control measures, which were mainly the application of malathion in a protein hydrolyzate bait (9). Even though the insect was found on a million acres, well scattered over much of Florida, the medfly was eradicated the following year. The eradication campaign cost almost $11 million.

Surveillance with the attractant-baited traps was continued. Reinfestations occurring in 1962 and 1963 were picked up by a powerful new synthetic called trimedlure (10). The incipient infestations were wiped out within a month or so at relatively small cost to the Government. U.S. Department of Agriculture officials estimate that the early detections saved the Government $9 million in potential eradication costs.

When an attractant is used for direct control, it is combined with a toxicant; the supreme advantage of this approach is that the toxicant hits the target organism. About a year ago, through the use of a specific attractant, Department entomologists eradicated the oriental fruit fly (Dacus dorsalis Hendel) from the 33-square-mile isolated

Pacific island of Rota (11). Small absorbent boards containing a combination of methyleugenol, a powerful lure for the male oriental fruit fly, and a potent insecticide, naled (or Dibrom ®), were dropped by airplane every few weeks. Responding insects consumed the odorous attractant and died by the millions. In a matter of months, the males were annihilated and the species on the island perished. Eradication was accomplished at a cost of only 50 cents an acre, including distribution. You can see the advantages of this approach even aside from the low cost. Only the offending insect is attacked. Wildlife is not affected. Insecticides are not spread needlessly.

These results indicate that we can look forward to the eradication of the oriental fruit fly on a larger scale; eventually complete eradication of this insect may be possible.

In 1885, Coquillett attempted to control grasshoppers in California with a poisoned bait (3). The experiment was a failure, but the idea recently has been successful (9). With the proper food lure, much less toxicant is required to do a given job than with insecticide alone, and complete coverage is not necessary because the insect comes to the lure. A clever adaptation of this technique has been used against the imported fire ant (Solenopsis saevissima richteri Forel). Mirex, a very slow-acting poison, and soya bean oil, a food lure, are dispensed on a granular carrier (corncob grits). The unsuspecting ants carry the granules into the colony nest and, as is customary with social insects, the food is passed throughout the colony. About 2 days later the poison takes effect and wipes out the colony. From 96 to 100 percent control was obtained with less than 5 grams of insecticide per acre (12). There was no effect on wildlife or fish and no contamination of milk or other food products. Needless to state, many foods and oils were evaluated in food acceptance tests before soya bean oil was chosen (13). We have to seek out these individual preferences, because this is what is required to selectively eliminate a species from a complex environment.

The food-based attractants supplement the powerful specific ones very nicely. The powerful lures help detect the insect; the inexpensive food lures, which do not require specificity or long-range action, cut down on the amount of insecticide needed and help in control or eradication.

The instances of success in the attractants field have not been easily won. It will not be possible to detail the enormous amount of technology that had to be built up before any of the cited achievements could be accomplished. However, several examples will illustrate the point.

The search for a synthetic medfly attractant started with empirical screening of many types of compounds and materials. To make this operation efficient, a rapid method of bioassaying large numbers of candidate materials was necessary.

The screening of attractants is by no means as straightforward as the screening of insecticides. The bioassay must be built around the idiosyncracies of each species (14). The olfactometer that measures attraction for the medfly is an 8-foot cubical screened enclosure that contains about a dozen chemically baited traps on a slowly rotating wheel. As in nature, the flies respond to the most attractive chemicals while in free flight.

Testing is further complicated by the effect of vapor concentration on attraction. The ideal lure will attract at high and low concentrations, but few chemicals act in this way. Instead they become repellent at concentrations that are too high and are not detectable at low concentrations.

In order to make good progress, a means of bioassaying insects the year around is most desirable. Laboratory evaluation makes this possible and greatly speeds up testing by eliminating all but the most promising chemicals. Field testing is a valid recourse; but it is time consuming, costly, and usually possible only during a limited part of the year. A means of rearing insects is needed to supply insects for the bioassay. Even when they are available, such rearing may be complicated by cannibalism, vulnerability to disease and parasites, appropriate diet, etc. Daily and seasonal variation, stage or age of the insect, as well as normal biological variation, all make the testing of attractants a far more sophisticated procedure than that of testing insecticides.

Then there is the persistence or attractive life of a chemical, the method of exposing it, and the possibility that the chemical may exist in several stereochemical forms, each of which may have a different degree of attraction (15).

Ultimately, the best attractants must be field tested because laboratory and field tests agree only qualitatively. In the field, attractants must prove themselves in competition with a multitude of natural odors, colors, light conditions, and weather.

Trap design is a study in itself for each species. The color, type and size of wick, amount of chemical, size of openings, and trapping technique must be determined (5). Even if all works well, unusual interferences sometimes occur. Ants were found to be stealing the trapped fruit flies, and an ant repellent had to be added to the trap. Birds also began stealing the trapped flies, and a screen, covering half of the trap opening, had to be installed. Even with the best design, improperly placed traps will not catch. Traps placed in hollows or in dense growth do not catch well owing to restricted air movement (5). The height of a trap makes a difference.

I hope that these few examples point up the great amount of research involved in using attractants successfully. Inasmuch as each species must be handled differently, you can see that much work awaits us even if our future efforts were to be simply a continuation or extrapolation of the techniques now being used for the few species for which we do have satisfactory attractants. However, what we do learn will undoubtedly speed up these future exploits.

Many insect species have the ability to reproduce rapidly and to establish incredibly large populations in a short time. Any means of depressing this enormous reproductive potential directly or indirectly is worth investigating. The insect sex attractant in facilitating the mating process falls in this category, and its value in preventing the spread of the gypsy moth through detection has already been mentioned. There is little doubt that sex attractants can help in the direct control and eradication of insects, but the very potent nature of these exotic materials makes it difficult to obtain enough of them for identification. For example, 500,000 abdominal tips of virgin female gypsy moths were required to get one small drop of pure sex lure, and it was only after about 20 years of painstaking chemical effort that the attractant was identified and synthesized (6). Because of these difficulties the identity of very few sex lures has been determined.

Sex attractants among insects may be more widespread than is generally realized. For example, about 2 1/2 years ago a conference on insect sex attractants, called by Dr. E. F. Knipling, brought together about 75 research workers. After receiving a briefing on what was known, they were asked to look for sex attractants among the species they worked with. About 25 species, previously unknown to have sex lures, turned up having them, and many of these are important pests. Again each species had its own idiosyncracies. The peak mating period of one--the southern armyworm [Prodenia eridania (Cramer)]--occurred between 3 and 5 a.m. During our usual working hours these insects are indifferent to their own sex attractant. The European corn borer [Ostrinia nubilalis (Hübner)] had to be viewed under infrared light to observe its mating habits. It mates in total darkness (16).

To date, more than 200 insect species have been reported to have sex attractants.

You do not have to be much of a prophet to predict that there will be a great upsurge in activity in the sex-attractant field. The need is there, we are learning how to use these materials, and the results have been rewarding.

Perhaps the greatest impetus to undertake such studies comes from the chemical field itself. New chemical instrumentation has made analyses and identifications of chemicals possible at levels down to 1/1000th of those previously possible. For example, mass spectral analyses with only 0.1 microgram have been reported (17). Gas chromatography is facilitating the isolation and purification of infinitesimal amounts of compound. The new instrumentation has also extended the range of chemical information that may be amassed, and in many analyses the sample is recovered completely. This outstanding progress in microanalysis has been recent and is largely due to the introduction of electronics into chemical equipment. We can expect our chemical capabilities to increase in the future and the identification of sex attractants to be correspondingly facilitated.

In spite of these wonderful advances, there is no chemical method known today that can compete with olfaction in terms of sensitivity and, in some cases, in detecting small differences in molecular arthitecture. The silkworm moth (18) [Bombyx mori (L.)], the gypsy moth (6), and the American cockroach (19) [Periplaneta americana (L.)] respond to a millionth of a millionth of a microgram or less of their respective sex attractants, and this amid the many odors in our environment. Our most sensitive analytical methods for an organic molecule require about a million times this amount. Nevertheless, the time is now ripe to tackle these sex attractant problems, and also to undertake the identification of other pheromones (20), which are the odorous substances of insect origin that control or affect insect behavior and development.

By spreading over a wide area the synthetic sex attractant gyplure, we have been trying for the past several years to jam chemically the female gypsy moth odor signals that attract the male (21). With the sex odor everywhere, the males should become utterly confused in their attempts to find females. They may additionally--because of the high excitement induced by the lure--become exhausted in short order, or because they are continuously exposed to the lure, they may become insensitive to it. If any of these reactions occur, the odor-guidance system, on which the opposite sexes depend for their mating rendezvous, will be impaired, and their ability to reproduce in great numbers should be depressed.

An attractive feature of this so-called "Operation Confusion" is that no toxicant at all is necessary.

Thus far, "Operation Confusion" has been unsuccessful; but we do not believe the idea has been properly tested yet. In 1961, we found out too late that the gyplure made by a commercial firm contained many impurities that were inactivating the lure. During the past year our group made 30 pounds of gyplure for tests to be run this past summer (22), but again the large-scale preparation was not sufficiently potent and the test had to be cancelled.

These difficulties led to some interesting studies. For example, attraction tests of cis and trans mixtures of gyplure disclosed that when more than 20 percent of the inactive trans-gyplure is added to the active cis-gyplure, the active material loses its activity (23). This is a serious problem, because the trans compound is the more stable of the two isomers and the shift to the trans form is always a likely possibility, especially during the preparation of large batches of the chemical or after dispersal of the chemical in nature.

However, this problem also brings up a most interesting possibility. If trans-gyplure were spread over a wide area, it might inactivate the natural lure given off by female moths. What is more, if this happens, trans-gyplure might be as much as five times more efficient than the attractive cis analog, because the trans compound seems to be able to inactivate about five times its weight of the active gyplure.

The attempt to confuse insects with trans-gyplure cannot be regarded as a new concept in odor chemistry, since it may be considered analogous to the masking of an unpleasant odor with another odor. You may wish to think of a masking chemical as saturating or fatiguing the odor sites so that these sites become insensitive to the sex attractant. This masking may be caused by a closely related compound and thus brings us to the possibility of trying in these confusion experiments compounds that are more readily available than cis- and trans-gyplure, e.g., ricinoleyl alcohol, its derivatives, and similar compounds.

The use of unrelated compounds for masking sex attractants is also likely, because the masking of odors by unrelated compounds is well known. Workers in this field speak of masking chemicals by anesthetizing odor receptor sites, of preferential solubility of chemicals at these sites, and of the possibility of displacing an odorous chemical with a nonodorous one.

The adaptation of electronics to the measurement of odor nerve potentials, that is the electrophysiological response to odors, offers great promise toward unraveling the complexities of odor phenomena. We have recently acquired such a setup at Beltsville, Md.

Monitoring the electrophysiological response of insect antennae to various odors will undoubtedly yield considerable information. A suitably wired American cockroach exposed to its sex attractant gives on an oscilloscope a characteristic signal called an antennogram (24). The gypsy moth antenna likewise gives a characteristic antennogram in response to its sex lure. Here we may have a fine tool for finding a chemical that will block the reception of the insect to its own sex attractant. By exposing a chemical and subsequently the natural sex lure, it may be possible to determine whether the chemical will block the response to the sex lure. It would probably be most fruitful to test compounds that are similar to the natural lure first. The compound that inhibits the action of the sex lure at the lowest concentration would probably be the most desirable, but it would have to be stable and readily available if it is to be useful in large-scale confusion tests.

The great amount of work and expense involved in isolating and identifying natural and synthetic attractants have been one of the most discouraging aspects of this type of research. If we find a potent lure, it is usually useful for only one species. Contrast this effort with the search for an insecticide, which is usually selected to combat as broad a spectrum of insects as possible. However, if we consider that the attractant, once found and properly used (25), is available for all future time, or that it may provide a means of safe pest control, the search is most decidedly worthwhile. Furthermore, we expect our tasks to become simpler as we gather experience in this new field.

Because knowledge of odor chemistry and biology can be most helpful in insect control, we can no longer leave this important field to a few dedicated scientists. Within the U.S. Department of Agriculture, steps initiated several years ago are being taken to explore odor phenomena of all types in depth. Fundamental and basic studies will be undertaken in a new laboratory to be built at Gainesville, Fla. The laboratory will be staffed with about 80 scientists and assistants. Entomologists, chemists, biochemists, physiologists, engineers, and various other disciplines will be represented. Their scope will extend from gross morphology to cytology, from stimulus to electrophysiological and behavioral responses, from secretory organs to sensing mechanisms; the entire physiological process will be scrutinized. They will study oviposition and feeding stimulants; chemicals from insects; and chemicals from plants, especially those that draw insects to our mutual food supply. Odorous chemicals involved in vital life processes of insects will be investigated. Odor threshold values, metabolism of receptor and transmission organs, odor synergism and antagonism, chemical structure versus odor and attraction can be studied; radiolabeling of odors may be useful.

In reading the literature one is soon struck by the frequent reference to our lack of knowledge of the olfactory process. Insects are excellent animals on which to develop our knowledge. Their organs of smell, usually located on the antennae, are not complex and are nicely exposed. The reactions of these simple and readily available creatures are likely to be automatic (26). Now consider the olfactory processes of the mammal. The receptor organs are complicated and difficult to get at (27). The response of a mammal is not likely to be automatic, but affected instead by its ability to learn, so that past experiences, pleasurable or otherwise, will affect the response (28). With our present knowledge of olfaction it is best that we start with a simple organism, such as the insect. Knowledge gained from these creatures may be useful in learning about our own olfactory apparatus, because knowledge of a small part can contribute to the understanding of the whole.

Whether the particular ideas or correlations suggested are useful or not, we can approach the truth by experimentation on these very simple beings. When enough data are developed, theories will be forthcoming and experimental criteria devised to test the theories. Such a course should promote progress in the field of odor chemistry.

Let me hasten to add that insect attractants will not solve all our pest-control problems, or even a major part of them, but they will undoubtedly become an important means of destroying our insect competitors safely. Attractants, as they are found, will help make all other forms of pest control more efficient.

With effective attractants, conventional insecticides can be directed at specific insect pests without hurting wildlife. They may also be combined with chemosterilants (29) for similar selective action.

And as we look to the future we do not plan to be content with 1964 pest-control efficiency either. Forward-looking entomologists are already radically upgrading their objectives and are now considering eradication of insect species very seriously. Attractants will help and will become more important as eradication becomes more likely. A good method for detecting infestations is almost a necessity to accomplish eradication and again a necessity to prevent reinfestation, or to establish quarantine lines. With international trade and traffic at an all-time high and increasing, accidental importations of harmful species are probably inevitable. This is why we are encircling our airports and harbor areas with attractant-baited traps; but we sorely need attractants to detect harmful species, for which we have not yet found good lures.

The screw-worm fly [Cochliomyia hominivorax (Coquerel)] was eradicated from Florida by overflooding the natural fly population with insects sterilized by high-energy irradiation. This technique, originally conceived by Dr. Knipling (30), is the only one that improves in efficiency as the insect population is depressed. Within the past year in the Pacific islands, the melon fly (Dacus cucurbitae Coquillett) has been eradicated from Rota and the oriental fruit fly from Guam by the same technique--overflooding with sterile insects. Through the use of the excellent attractants we have for these species (31), the insect population could be monitored, and with this information the overflooding ratio could be calculated, progress assessed, and the areas requiring treatment designated, until the last insect was destroyed.

I would like to leave this major thought with you: Attractants can help us use insecticides or other insect-control measures more efficiently and more intelligently.

May I conclude by stating that I see no "Silent Spring" ahead. If the productivity of our scientists today is any criterion, we can be confident that the human mind will come forth with new concepts and new tools and techniques that will assure for our people nourishing, healthful food unblemished by insect attack.

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THE ROLE OF CHEMICALS IN CONTROLLING PLANT DISEASES

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Tremendous strides have been made in controlling plant diseases by chemical means in the past three decades. The fungicidal activity of the alkyl dithiocarbamates was reported in 1934, and within 6 years the quinone fungicides were discovered and introduced into commercial use.

These discoveries pointed the way to breathtaking possibilities in plant disease control. No longer were agriculturists to be restricted to inorganic ions or molecules of copper, zinc, sulfur, and mercury, where about the only possibilities for improvement lay in changing solubility. With the advent of organic fungicides it became possible to design molecules to the exact specifications desired. There were almost limitless nucleophilic groups that could enter into and immobilize or retard biochemical processes of the cell. By proper modification of such active components, or addition of substituent groups, it should be possible to modify the physical-chemical attributes of a class of fungicides so it would become more, or less, selective in its action, capable of penetration into the living cells, safe for use on specific crops, persistent on foliage and fruit, resistant to erosion by wind and rain, photolabile, etc.

Three decades and 200,000 compounds later we are sadder but wiser men. The dream did not fail because we have marvelous materials, such as the alkylene bis-dithiocarbamates, quinones, imidazolines, *s*-triazines, captan, dodine, and an assortment of other heterocyclic nitrogen and sulfur compounds to choose from. However, the harsh facts are that probably no more than 40 million pounds of these new chemicals are being used on the 358 million acres of cultivated land in the United States. Very few of our 8,000 fungus diseases are controlled satisfactorily and scores of them not at all. We produce more and better crops with less damage than heretofore, but we still suffer staggering losses.

Wherein have we failed to live up to our responsibilities and opportunities? We need to know why we have not attained the brave new world of our dreams of 1940. To this end we would like to look at the magnitude of our practical failure, the useful new knowledge gained and how it can be used, and to briefly explore some new approaches that could be taken in facing up to the future.

CURRENT FAILURE TO MEET DISEASE PROBLEMS OF CROPS

No one knows exactly how much damage is done by any one disease in any one locality, much less what the aggregate losses may be from all diseases of crops in the United States. Reasonably good, educated guesses can be made from balanced judgment based on many observations of the gains that ensue when disease-control methods are practiced alongside untreated plots or fields for a number of years or when general yields are compared in disease-infected and healthy fields in different localities or years. A recent compilation of such balanced judgment of authorities in the United States has been summarized by LeClerg (14) for the losses during 1951-60. The final bill totals $3.6 billion per annum, which would seem to be a reasonable estimate. A full warning must be made that if all this lost crop productivity, equivalent to the yield from 30 million acres, were dropped in the marketplace, it would further depress prices disastrously so these dollar values would not be realized. Probably the best way is to look at this as a loss of over 8 percent in efficiency on the farms in use of human labor, equipment, fertilizer, seed, and soil resources.

The percent loss in field crops averages about 12 for cereals, 16-23 for sugar crops, 11 for tobacco, pasture crops about 5, hay 15-24, fruit crops 2-34, with the principal pome and stone fruits suffering 8-17, and vegetable losses 2-22, with principal crops suffering 10-20. The specific causes of this damage will not be published until 1965, but it is well known that the blights, scabs, fruit rots, and cankers are major causes of loss even though there are effective chemicals for them.

The losses on field crops continue to be heavy, because sources of disease resistance in resistant varieties are being continuously broken down by evolution of new parasitic races of pathogens, and the returns per acre on these crops are not sufficiently large to justify the relatively heavy cost of repeated applications of protective chemicals. Stakman and Harrar in their book on "Plant Pathology" (31, p. 507) stated that black stem rust of wheat has been adequately controlled in no more than 20 years between 1904-54 because of the rapid succession of races. In general, the obligate parasites, such as the rusts and powdery mildews, continue to be major disease problems.

Probably the largest unresolved disease problem is the root rots caused by a variety of fungi and bacteria aided and abetted, on occasions, by nematodes. These relatively unspecialized organisms are inadequately deterred by natural resistance of their hosts because of the pathogen gaining access through wounds and other breaches in their protective devices of the plants, prolonged extension of the susceptible juvenile condition during adverse weather conditions that prevent escape, and the high cost of treating soils with chemicals ($50 to $400 an acre).

There is no way to estimate what the crop losses would be if chemicals were not available. It is known that many fruits and vegetables simply could not be produced in the areas best adapted to them. Acceptable apples would not come from 60 percent of the present area, peaches could not be grown in the Southeast, and potato culture would be driven inland to the higher, dry plateaus by late blight (Phytophthora infestans). Many of the relatively successful blight-resistant varieties would fall if they could not be protected under duress of environmental conditions. The real issue before scientists is not how much crop insurance is now being bought by chemicals but why we are still losing about $3.6 billions annually! Has everything possible been done to find reasonably efficient, reliable control measures by perfecting chemical devices, cultural practices to promote biological control, or breeding resistant varieties? Obviously since we have not done much more than establish a bulwark to keep our crops from utter destruction, much more skill is needed.

PROGRESS IN DESIGNING MOLECULES

A substantial volume of data has been accumulated on the relationship of chemical structure to activity. There is little need to go into great detail, because the subject has been reviewed adequately by Horsfall (7, 8, 9), McCallan (16), Sexton (29), Rich (25), Sisler and Cox (30), and Owens (20), who give citations to the original research. A few selected examples will serve to illustrate the major points.

The mode of penetrating cell walls and membranes has not been fully explained. However, it is obvious that many of the major achievements with fungicides have come about by designing molecules that penetrate rapidly. Miller et al. (19) have shown that a material such as glyodin is taken up rapidly against a concentration gradient so spores will contain over 21,000 p.p.m. in 2 minutes. The membranes of the fungus spore apparently are impaired, as shown by the outward movement of solutes from the cell and by more rapid uptake of chemicals after exposure to silver. A similar effect was obtained with symmetrical triazines by Burchfield and Storrs (3).

There is substantial evidence that the molecule must have a proper balance between lipophilic and hydrophilic properties in order to achieve satisfactory permeation (26). These properties may be affected by use of an alkyl chain of 17 carbons, as in heptadecyl imidazoline (34) and substituted tetrahydropyrimidine (24), or 8 carbons on ethylene thiourea (27, 28), a parachlorophenyl group, as in the nitrosopyrazoles (18), and possibly a trichloromethyl group, as in captan (9, 11).

There may be much more to this process than simple lipid solubility, which would permit the molecule to pass through the lipid phase of a cell membrane if the Danelli concept applies to fungus membranes. It is entirely possible that breaking of hydrogen bonds or van der Waal's forces between lateral protein molecules of the membrane may be the primary prerequisite to creating a breach into the wall of the membrane, and that there is sufficient dislocation in the lipid layer underneath to create a small pore. It is obvious from the studies cited above, as well as many others, that the integrity of the membrane is ruptured and penetration is not a simple diffusion process of molecules dissolved in an aqueous or lipid medium.

There is a confused state of mind as to what happens once the molecule reaches the cytoplasmic fluid. Many types of molecules are either degraded or bound to metabolites rather rapidly, but they do enter into reaction with a wide assortment of enzyme systems. Reaction with sulfhydryl and amino groups of enzymes can be demonstrated in vitro or in vivo fairly easily, but exactly which biochemical process is disrupted sufficiently to result in death of the spore is not easily determined. Owens (20) has reviewed several aspects of this problem and cites other commendable reviews. Very suspect among the reactions that take place are blocking of the normal phosphate metabolism and disruption of the Krebs cycle before citrate can be formed from acetate by interference of strong oxidants with coenzyme A. This mechanism has been studied carefully for ferbam and thiram where a series of transformations seems to occur. However, reaction with the thiol group of coenzyme A would seem to be involved (23), as it is in captan (21) and dichlone (22). The significance of this site of reaction has been confused by other observations on the inhibition of aconitase necessary for metabolism of citrate and blocking of a variety of other enzymes necessary for formation of pyruvate and other essential constituents of the cells (30).

Several essential chemical mechanisms are being exploited in bringing about the destruction of these enzymes. Among these are chelation of essential metallic ions, alkylating reactions, and interference with the electron transport system.

The idea proposed by Zentmyer (35) in 1944 that fungicides could operate by chelating essential bivalent cations, such as zinc, has been subject to debate. The idea is fundamentally sound but is confused considerably by the fact that the copper chelate of oxime is more active than unchelated oxime. On the surface this appears to refute the suggestion, but supplementary hypotheses have been advanced that the 2:1 chelate promotes penetration of copper and then dissociates inside the cell to release both a copper toxicant chelated 1:1 and a molecule of oxime ready to chelate trace elements inside the cell. Since the chelation constants and competition of different metals for chelation sites will vary with the supply of electrolytes and cytoplasmic reaction of the cell, the final answers have not been obtained.

A fresh approach to the problem is being taken by Gershon, who has synthesized a number of mixed chelates with different dissociation constants. Not only can the amount of dissociation in the cell be controlled, but one of the end products will be essentially inert as a fungitoxicant, so it is hoped that by study of uptake and fungitoxicity of these compounds (6), new information can be obtained on the validity of theories proposed to date. Undoubtedly there is potential capacity for chelation as proposed by Zentmyer, and it should lead to fungitoxicity, provided there are no rapid detoxication processes nor other toxicant mechanisms of reaction by the quinolinol compounds in the cell environment. Other potential chelating agents, such as the dithiocarbamates, enter into other reactions that are known to supersede any removal of metal catalysts (20).

Several of the new fungicides probably operate as alkylating agents. Among these are the halogenated compounds that react readily with amines, thiols, and nucleophilic compounds by substitution reactions, Dichlone, for example, will react with functional sulfhydryl or amino groups to inhibit many enzymes, such as dehydrogenases, carboxylases, and coenzyme A. The very thorough study on the kinetics of the alkylating reaction was made by Burchfield and Storrs (2, 4) on 2,4-dichloro-6-(o-chloroanilino)-s-triazine (Dyrene) and 1-fluoro-2,4-dinitrobenzene. Rates of reaction with a number of cell metabolites at different pH values give a clear interpretation of how these materials would compete for receptor sites in the normal cell environment.

Interference with the electron transport system of the cell probably is more widespread than is given credit. Elemental sulfur has long been known to be reduced to hydrogen sulfide when brought into contact with living surfaces, probably by enzymatic action. This probably occurs by a single electron transfer from donor in the cell to the sulfur as described by Owens (20), when the eight-membered sulfur molecule undergoes ring cleavage into a polysulfide chain. The reduction of sulfur leads to the release of a molecule of carbon dioxide from the fungus spore for every molecule of H_2S produced (17).

The decarboxylation processes that lead to carbon dioxide evolution could better be explained as a result of the fungitoxic reaction rather than as the primary cause of fungitoxicity if electrons are being diverted from the regular electron transport system. This would reduce the amount of ATP formed and lead to rapid starvation of the spores, according to Tweedy (33), who found only 7 percent of normal incorporation of ^{32}P into RNA and DNA in spores of Monilinia fructicola when sulfur was being reduced to H_2S. His data show that amino acids are deaminated, ammonia collects in the spore, and respiration is accelerated, thereby suggesting that the amino acids are being catabolized via the Krebs cycle. The most logical point for suspecting diversion of electrons from the transport system would be between cytochromes b and c. If his theory stands up, we will have at long last a valid understanding on the mechanism of action of sulfur--the oldest of all fungicides.

The growing volume of information on the design of molecules, which will penetrate the fungus body or be sorbed to it and enter into specific reactions fatal to it, has served to orient the thinking of chemists and plant pathologists toward the design of more effective molecules with greater selective action. However, much of the search for better compounds must still be done by empirical testing. There are too many imponderables both in the living cells and in the nature of new molecules to predict exactly what will happen before they are tested. The gain in efficiency of research from the fundamental knowledge obtained is more than offset by the increase in standards of performance expected of new materials.

It is relatively easy to find a compound with a reasonable degree of fungitoxicity, but it is very difficult to find one that can be used for crop protection as they are now used. The necessity of obtaining low phytotoxicity, low mammalian toxicity, reasonable retention in face of erosion from environmental forces, and securing reasonable protective films without excessive residues at harvest cause a high mortality of new compounds.

In spite of this, new compounds, such as dodine, are being discovered and developed to fill the unmet needs on the farms. The most recent of these is tetrachloroisophthalonitrile. Turner et al. (32) report exceptional fungitoxicity in this preferred member of a series and performance equal or superior to that of a large number of successful products now being used commercially on a wide assortment of fungi.

PROBLEM OF SOIL-INHABITING PARASITES

None of the major crops escape damage from soil-inhabiting fungi, bacteria, and nematodes. The root rots, collar rots, damping-off, seedling blights, and wilts take a toll every year. Some of them are so chronically omnipresent that losses are accepted year after year as almost a normal effect, and complaints are raised only when weather conditions favor an extremely severe infestation. Only moderate progress has been made in developing chemical aids for their control. To obtain the required 100 p.p.m. or so of toxicant in the upper 6 inches of soil (2 million pounds per acre), approximately 200 pounds of chemical are required. In actual practice, 20 to 400 pounds are used, but up to 3,000 pounds would be required to suppress the more resistant species of fungi.

The obstacles against suppression of these soil inhabitants are formidable. Soil fumigants are lost by volatilization. There is substantial loss due to adsorption onto clay and humus particles. The amount of sorption loss will vary with the nature of the clay fraction and the compound used (5, 13). The nonpolar chemicals, such as ethylene dibromide, are less readily sorbed on montmorillonite than on kaolinite or illite because of differences in the particle surface. Cations are generally adsorbed on the outer shell of clay micelles, and the degree of anion sorption is affected by the ratio of silicon to aluminum or iron, so soils with kaolinite or illite clays should sorb anionic materials most readily. Thus, every soil presents its own peculiar problem in arriving at a suitable dosage level. The factors behind soil treatment have been summarized very well by Kreutzer (12, 13), Domsch (5), and Kendrick and Zentmyer (10).

In addition to the problem of obtaining a suitable dosage at reasonable cost, there are two other interlocking problems regarding soil disinfestation. The first is an adverse effect on beneficial soil micro-organisms. The microbiological balance may be upset to such an extent that it takes weeks to months to recover. One of the adverse effects is suppression of *Nitrosomonas* and *Nitrobacter*, so that nitrification is seriously impaired. There may be serious accumulation of ammonium in treated soils since ammonification is not seriously impaired. There is also a tendency to impair agglomeration of soil particles by micro-organisms, so texture of soil may be impaired slightly by some of the soil treatments.

The second problem is reinfestation of treated areas by windborne or mechanically transported inoculum. There is a strong tendency for the number and assortment of micro-organisms to be sharply curtailed by fumigation, so survival of pathogens or their reintroduction may lead to a destructive reinfestation. The fungi that operate as normal soil inhabitors seem to be particularly resistant to disinfection. Fortunately since some of the normal antibiotic-producing organisms, such as species of *Streptomyces* and *Trichoderma*, survive equally well and often build up in numbers very rapidly in the posttreatment period, they probably serve to hold the pathogens in check during the period of population recovery.

PERFECTION OF PERFORMANCE BY FORMULATION

Fungicides are used predominantly as crop protectants. The purpose is to place them so they will be available in overwhelming concentration when the pathogen comes in contact with them while seeking an infection court. There are several reasons why a minimum deposit of chemical has been sought in achieving protection. As a simple matter of economics, the smallest possible dosage was recommended. The value of efficient application to avoid excessive dosages was increased when agriculturists shifted from the relatively inexpensive inorganics to carefully designed, expensive organic compounds. Furthermore, there was always danger of injuring the crop by excessive application, especially when substances of high biological activity were being used. The need for the least possible residue to achieve the maximum protection for the plant has become even more critical in recent years as a means of meeting the legal requirements for safeguarding public health and avoiding needless dislocation to the biological forces in nature. Very few fungicides have been criticized or even been very suspect for damage to man, domestic animals, or wildlife. The only serious exceptions have been the organic mercurials used as seed treatments and to a limited extent in orchard spraying. However, this does not excuse use of the most conservative dosage commensurate with effective crop production.

A careful analysis of the relation of particle size to protection by dichlone by Burchfield and McNew (1) revealed that there probably is an optimum particle size for a protectant fungicide. A minimum amount of particle surface should be exposed to obtain the desired protection of vulnerable surface of leaf and fruit. If too much surface is exposed by grinding particles too fine, the deposit is susceptible to erosion, volatility, photodecomposition, and other debilitating forces. If the particles are too large, an inordinate amount is required to cover the surface adequately. Contrary to the prevalent idea that the particles should be made as small as possible, these studies indicate that size of particle should be adjusted to the best intermediate level by balancing off several factors of fungicidal efficiency, physical properties of the molecules, nature of surfaces to be protected, environmental conditions under which the material would be used, and persistence of chemical desired. It follows that every crystalline material probably would have a different optimum size of particle, and under some conditions of great lability the particles should be of several sizes so each would be available to control the fungus at different periods of time.

In addition to particle size, many factors should be taken into account in designing the perfect protective spray formulation. Surfactants must be used to obtain spreading and adhesion to the surfaces. Unfortunately the nature of the chemical being used, the hardness of water to be used, and the nature of the plant surface to be protected all must be taken into account in deciding on whether a cationic, anionic, or nonpolar surfactant should be used. Sometimes deposit builders or solvents to speed up penetration or permit emulsification are used.

The formulating materials for use in soil disinfestation are equally important. It is possible to disperse materials in cosolvents that will speed up penetration of the soil and the micro-organisms in them and to assure ready dispersion in the soil. Water solubility and volatility can be controlled in acidic materials by converting them into salts or esters or otherwise formulating them so they would be adsorbed on clay particles. They could, therefore, be made to persist in the top few inches of soil until they could achieve partial sterilization in this zone most frequently inhabited by the soil microflora.

POSSIBLE NEW APPROACHES TO USE OF CHEMICALS

There is no room for complacency as long as the farms are sustaining such large losses of crops and the present materials have to be applied repeatedly and in relatively heavy dosages to protect crops. The present system of screening compounds to locate new types of activity will continue to yield better, new compounds just as it is now doing. However, we need materials that could operate in more subtle ways, be applied less frequently or in smaller dosages, or could exploit advantageously the peculiarities of the pathogen, host, or environment to bring about the desired effect.

There are no really satisfactory control measures for virus diseases except sanitation and breeding of resistant varieties. Once a crop becomes infected it is lost regardless of whether it is an annual or in a mature orchard or grove of perennials. Many species of fungi escape contact or are resistant to the chemicals now being used.

Design of Unstable Molecules

Much progress has been made in using unstable sulfur compounds. The outstanding success has been with nabam, which is essentially inactive against fungi. The inert deposit is converted to alkyl isothiocyanate, probably by way of ethylenethiuram disulfide and ethylenethiuram monosulfide (15). The active fungicide is very labile and never accumulates in amounts sufficient to be phytotoxic. This is an ideal situation, because the toxicant is ephemeral and the system that generates it is exhausted in 5 or 6 days, so there can be no residue to harm either the crop or the consumer. Something of a similar nature probably occurs when Vapam and Mylone are used, since they seem to be converted to isothiocyanates.

So far no one has succeeded in creating an inert molecule that is rendered fungitoxic only after penetrating the fungus body. One of the very distinct possibilities would be to seek materials that would be subject to beta oxidation in the fashion that the selective, hormonal herbicide 2,4-D is derived from the inactive butyric acid homolog. The 2,4-dichlorophenoxybutyric acid (or butanol derivatives) can be converted into 2,4-D only by those plants that have beta oxidases, so these, in substance, commit suicide after taking the material into their cells. It is known that some valuable crop plants, such as alfalfa, do not have β-oxidases and still others, such as wheat, are deficient in α-oxidases, so much materials with a nitrile group in place of the carboxyl group would not be phytotoxic but would be injurious to any fungus with α- and β-oxidases. Because of the intense lipid chemistry in plant pathogenic fungi, it would be logical to expect them to have β-oxidases.

There must be a multitude of such materials that could be developed if only sufficient thought is applied in this direction. These unstable molecules would be the ideal sort to design from all viewpoints. No poisonous residue would be in the environment, hazard to crops without the oxidizing enzymes would be minimal, and the toxicant would not occur on food products, so residue tolerances could be eased a bit.

Development of Systemic Toxicants

Evidence is appreciable that some of the fungitoxicants can be taken in and move as systemic toxicants inside plant tissues. However, most of the protective fungicides have been designed to have the wrong physical attributes to survive in the cytoplasm. Since they are chosen for low solubility in water and for high chemical reactivity, they are prone to remain fixed in one spot and to react so readily they are detoxified very promptly. However, if relatively simple toxophore groups were attached to known mobile metabolites containing a generous supply of polar groups, such as one would find in an amino acid, the mobility might be enhanced substantially.

Most persons automatically think of chemotherapeutants as being taken up by the roots and transported through the tracheal tubes, where they could destroy the wilt fungi and bacteria, or to the leaves, where they could prevent foliage and fruit infection. However, the opposite route offers even more promising possibilities if someone could develop a material that would penetrate the leaves through cuticle, stomata, or hydrathodes and pass into the phloem and be exuded by the roots. Such materials could change the rhizosphere either by serving as toxicants or by modifying the competition between micro-organisms in this vital area, where the soil-inhabiting pathogen must first establish itself. It is known that certain cell metabolites may take this route and affect soil micro-organisms within 2 or 3 hours after a molecule of ^{14}C is taken in by the leaf. It should be possible to design organic phosphates that would be ideal for destroying nematodes by this route. The problem is to make the molecules sufficiently stable to endure the rigors of the route without accumulating as harmful persistent residues in the plant tissue.

If toxicants cannot be developed for such purposes, it is potentially possible to change the secretion of normal metabolites in the soil. For example, antibiosis in the soil could be stimulated against Texas root rot (Ozonium omnivorum) by stimulating carbohydrate secretion from the roots during midseason so antagonistic bacteria would create a protective zone around the root hairs just as is done around seedlings early in the season before growth and food storage rob the roots of food reserves. More information is needed on the forces operating in the rhizosphere of all plants subject to root invasion. It is known, for example, that pea varieties resistant to the near wilt Fusarium secrete materials toxic to the fungus, whereas secretions from susceptible varieties stimulate its growth, but the materials responsible for this biological control over the pathogen have not been isolated. They might provide valuable leads to the synthesis of systemics that would not create harmful residues.

Stimulation of Natural Antibiosis

Stimulation of natural antibiosis in the soil has scarcely been exploited. In addition to changing the rhizosphere, as discussed above, it is possible to alter the soil environment so it encourages harmless saprophytes at the expense of pathogenic fungi and bacteria. Many of these are poor soil competitors and would die out if the saprophytes were encouraged to grow. It has been well established that some of the purified antibiotics are potent fungicides, but they are not suited for use in soil either because they adsorb on clay and are rendered inactive, are decomposed by soil micro-organisms, or are too phytotoxic or too expensive to be used at the dosages required. The genesis of such materials in the soils by antagonistic soil micro-organisms is a much more promising solution to the problem.

Several moves have been made in this desirable direction. One of these is to plow under crop refuse, green manure, or livestock manure to stimulate growth of saprophytic bacteria. Such measures have proved effective in reducing the severity of strawberry root rot, Texas root rot, and other root-infecting fungi. It was only one step from this observation to the addition of sugar for the strawberry root rot, since glucose- and sucrose-requiring bacteria inhibit the fungi responsible for the trouble.

A second possibility exists in observations made on changes in the microflora following soil disinfection. As a general rule, the pathogenic fungi that are not regular soil inhabitants but manage to survive in crop refuse are destroyed rather readily, and the more aggressive pathogens require heavier dosages or more active disinfectants. In keeping with this scheme of things, the soil saprophytes that are indigenous to the soils often escape the treatments designed to destroy the pathogen (13). Among these are the Actinomycetes and Streptomyces spp. that have exceptional ability to produce antibiotic substances effective against a wide assortment of fungi and bacteria. Even more resistant is Trichoderma viride, the fungus that produces glyotoxin, which is strongly inhibitory to fungi.

There are two good reasons why these studies on shifting the character of soil populations by chemical treatments should be investigated much more thoroughly. There is always the possibility that standard fungicides would do irreparable harm to the soil by injuring desirable micro-organisms, such as the nitrogen-fixing bacteria, the legume nodule bacteria, or the antagonists of plant pathogens. The extent to which these changes are going to be induced should be explored very carefully in different types of soils. In addition, a search should be made for selective organic chemicals that would stimulate antagonists for plant pathogens either nutritionally or by releasing them from competition with their coinhabitants of the soil. The screening methods now employed for locating soil disinfectants are not designed to exploit the possibilities of soil antibiosis, since they are aimed solely at locating fungicidal action. However, there are distinct possibilities in trying to harness this force to kill out less well-adapted pathogens rather than to attempt their destruction by massive application of fungitoxicants.

Regulation of Plant Resistance

Regulating plant resistance is a distinct possibility for future research. Already there is good evidence that wilt diseases, such as the Dutch elm wilt (Ceratocystis ulmi), can be alleviated by use of chemicals that change the nature of tracheal walls. It is rather clear that this fungus is destructive only early in the season when new tracheal tubes are being proliferated, and once these become lignified, the plant may recover sufficiently to survive the season and years ahead with walled-off infection.

A more interesting possibility for future use of chemicals for changing hereditary patterns of susceptibility in crops is coming over the horizon of science. The new knowledge on the chemistry of hereditary control over cell activities reveals that the deoxynucleic acids (DNA) control inheritance from the nucleus, and the ribonucleic acid (RNA) carries the DNA code to the sites of protein synthesis, which are essential for formation of the enzymes that direct biochemical processes. The methods of synthesizing polynucleotide compositions on a sugar-phosphate chain are available, and methods of regulating the sequence of the four nucleotides on that chain are at hand.

If one is allowed to postulate that plant viruses operate by having their RNA enter competitively with normal messenger RNA into combination with ribosomes to form a new polysomal complex, then it is possible to visualize methods of interfering or destroying virus activity by introduction of new types of

RNA into the cell. Such RNA could be of synthetic origin. Furthermore, the obligately parasitic fungi of the Uredinales, Erysiphales, and Peronosporaceae, which number among their members many of our most destructive and least effectively controlled plant parasites, may be dependent on host RNA for their metabolic activities. If so, they could be very sensitive to treatment with synthetic RNA once the proper code could be developed to affect them but not the host plant.

It is obvious that the type of molecules required will be very complex in nature, and it will be difficult to obtain their permeation of living cells without destroying cytoplasmic functions. However, since there is a wealth of information on inoculation procedures with plant viruses and since the use of foreign nucleotide chains to change the carbohydrate metabolism of bacteria has been achieved recently, the idea is not absolutely impossible. It is already known that certain forms of viral RNA can be used to render a plant immune to infection by other viruses closely related to them, and resistance to fungi can be enhanced by viral infections, such as virus Y increasing resistance of potato to the late blight fungus Phytophthora infestans. Furthermore, it is known that some plant viruses multiply regularly in plants without causing visible symptoms or reducing growth (potato virus X, ring spot of tobacco secondary infection).

Still farther over the horizon lies the possibility of using synthetic DNA as an artificial gene to change heredity of both crops and pests. The potential danger of such experimentation is obvious, but the advantages are equally impelling. Many plant pathogens produce new races regularly, and it is only a matter of time until some of them circumvent the known genes for resistance in the crop species. By intensive inbreeding and hybridization of crops, the plant breeder has been discarding genetic versatility in our domestic species of plants, which render them susceptible to large deviations in climate or attack by pests. The time may very well come when such genetic diversity will have to be reestablished by chemical means.

Of course, the unraveling of the nucleotide code behind gene action will require a tremendous effort, because up to 6,000 nucleotide groups may be involved in each gene. Experimentation would obviously have to start with simpler molecules unless partial biological control can be used in the synthesis of the proper nucleotide sequence. This might be achieved to a large measure by the marriage or matching technique of RNA and DNA on a cellulose column.

POSSIBLE ROLE OF BIOLOGICAL CONTROL

In the foregoing discussion on chemical aids to plant disease control, emphasis has been placed on the use of materials under man's control to meet crises in crop production. These techniques, of course, are to be applied in conjunction with the best possible horticultural practices to escape, suppress, or circumvent the effects of parasitic attacks. It is doubtful whether any chemical control measure could be fully effective under the most adverse environmental conditions with a maximum inoculum potential of the pathogens operating in the habitat. Certainly control under such conditions would require such massive dosages at repeated intervals that the treatment would be economically unsound and potentially hazardous to an already weakened crop and the desirable biological forces of the environment.

The question may be asked fairly as to why all plant diseases should not be controlled by biological means. It is well to point out that plant pathologists probably spent about 95 percent of their effort between 1866 and 1940 trying to work out the biological factors behind the causal nature of disease, the capacity of the host to resist or recover from parasitic attack, and to exploit this knowledge in plant disease control. The tremendous volume of knowledge obtained is being put to use every day in the United States in choosing as nearly disease-free localities as possible, rotating crops to suppress pathogens, use of disease-free seed, proper fertilizer practice to promote disease-escaping and recovery processes, stimulation of soil antibiosis by proper soil amendments, choice of proper time for seeding, sanitary practices in propagation and harvesting, use of disease-escaping and resistant varieties, etc. These essential devices often have the great advantage of being the most economical and least difficult to incorporate into an agricultural program. Certainly there should be no easing up of the effort in these directions, because we have broader concepts and new techniques for advancing the knowledge on biological control today.

However, the plant pathologist has been sorely disillusioned by the results from this effort. The great varieties that were bred to complete immunity have fallen by the wayside like leaves in the fall as new races of the parasite have evolved. Perfectly sound recommendations regarding cultural practices to promote aeration of tops and suppression of inoculum fail at the most awkward moments in some seasons.

The truth of the matter is that all biological controls are designed to operate on a set of premises that certain normal or average conditions will prevail wherein there will be a balanced condition between pathogen, host, and environment. Unfortunately this condition rarely prevails year in and year out. Change is constant in all three of the components we are relying upon. The crop plant may be held in a susceptible juvenile state by retarded seasonal developments. The low population of soil micro-organisms suddenly gets a new lease on life, and they multiply wildly when there is excess rain to remove natural toxicants or to force the use of heavy nitrogen fertilization to keep the crop vigorous. The virulence of the pathogen changes because of mutation or reshuffling of its genes during sexual reproduction.

Unfortunately there is no such thing as a perfectly balanced biological state that can be depended on year after year. The best the scientist can do is to accept the parameters of variability that will prevail 70 or 80 percent of the time and work within these limitations. He tries to be ever alert to the shifting abilities of the pathogens, be it ability to attack a supposedly immune variety of the crop or to be susceptible to the chemical toxicant used in its environment at the most susceptible stage of its life cycle. Finally, he must be prepared to apply emergency methods to meet the unusual circumstances that are certain to prevail the other 20 or 30 percent of the time. The chemical controls, therefore, are the form of crop insurance that are indispensable in crises.

Because of these basic considerations agriculture will never be able to dispense with chemicals. In the future they will be used more--not less--to control plant diseases. This flat prediction is made because (1) we are still sustaining over $3 billion damage a year; (2) the best laid biological measures have a unique way of breaking down in a crisis and need a helping hand; (3) crop rotations are being shortened as cash crops become more important in farm economy with high fixed prices; (4) soils are being overworked so unbalanced conditions prevail both as to microbial population and nutritional components; (5) crops are being grown so intensively in specific areas to facilitate the modern requirement for economical processing and preservation that they are more vulnerable to attack; (6) crops have been bred to such high standards of uniformity that every change in the pathogens becomes a disaster that cannot be tolerated under modern farm economy, where heavy capital investment must be made to pay off every year if financial ruin is to be avoided; and (7) present marketing practices are so dependent on a uniform productivity of high-quality produce that appreciable fluctuations in volume of crop work to the disadvantage of both the farmer and the consumer.

The great problem today is to keep the research on fungicides and other disease-controlling chemicals progressive. There is no need to apologize for what has been achieved over the past 30 years, because it has been tremendous. However, great need still exists for better disease control. It can be met by a combination of traditional chemical research and opening our minds to the new possibilities knocking on our doors. The greatest mistake that could possibly be made would be to go on blindly screening compounds without exploring the possibilities of harnessing other forces of the environment and the crop to solve the problems.

The industrial chemist is confronted with a tremendous challenge. So are the academicians of research, for they have failed to keep fundamental knowledge abreast the battlefield. We cannot be proud when we simply do not know how a molecule permeates a spore, what the composition of a fungus cell membrane may be, which lipids exist in a fungus and where each is located to affect the availability of a fungicide, what the major and auxilliary biochemical processes are in the major plant pathogens, how a virus operates biochemically, what makes a fungus obligately parasitic or what forces of microbial competition operate against plant pathogens in the soil, and what the genetic code for disease resistance must be. If we knew these things, molecules could be designed to meet the practical demands of agriculture. Possibly molecules would be developed that could be more selective in their action, less persistent in the environment, and less suspect of hazard to man, domestic animals, or the environment. The opportunities for service lying ahead are exhilarating, but they will be realized only by acquiring the basic knowledge outlined above, and much more, to guide the research effort that is needed.

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THE FUTURE ROLE OF CHEMICALS FOR CONTROLLING PLANT NEMATODES

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Plant-parasitic nematodes have been responsible from the very beginning of agriculture for devastating losses to man's food and fiber crops. However, it was not until the mid-19th century that man was able to recognize these pests that for so many years had remained hidden in the soil and concealed within plant tissues. Since the first discovery of root knot on cucumbers in 1855, scientists throughout the world have made remarkable advances in describing hundreds of species of plant-parasitic nematodes and in defining their destructive role in modern agriculture. Nematodes are recognized as important pests of crops throughout the world. Our growing knowledge proves nematodes responsible for even greater losses than were first attributed to them by scientists.

Without the use of modern nematocides and nematode-resistant crop varieties, losses caused by nematodes would probably exceed 10 percent of our annual crop production, and under some conditions highly susceptible crops would be virtually destroyed. Several types of nematodes are responsible for low soil productivity through their many direct and indirect activities in soil and within plant tissues. Their activity is often responsible for an increased incidence of plant diseases caused by pathogenic bacteria, fungi, and viruses. By impairing root systems, nematodes are also responsible for inefficient use of both major and trace elements. The incipient damage to plant roots caused by nematodes frequently necessitates costly application of supplemental irrigation and side dressings of fertilizer nutrients to compensate for the disfunctional, mutilated roots of infected plants. Complete knowledge of the role of nematodes in reducing soil productivity will, in heavily infested soils, require reevaluation of our fertilizer, seeding, irrigation, and management practices before our farmland can reach its full potential.

Plant-parasitic nematodes occur in most soils. They may become a severe problem when the land is intensively cultivated. Unfortunately modern farming practices, which require frequent, intensive production of a limited number of crops, favor the rapid increase of these pests. Although good soil and crop management practices usually reduce nematode damage, the best practices designed for nematode control often are not economical; or they are not entirely successful or practical for controlling all types of parasitic nematodes. Under these circumstances, the use of nematocides provides the best practical means of controlling many nematodes.

USE OF NEMATOCIDES

Nematocides are used, at least to a limited extent, in the production of crops in every section of the country. The importance of controlling nematodes on tobacco was realized many years ago, and, in 1964, about 75 percent of our total tobacco acreage was treated with nematocides to control root-knot and other nematodes. Hundreds of acres of sugarbeets are grown each year on land chemically treated to control the sugarbeet nematode. Soil fumigation has been an accepted practice in the production of pineapples in Hawaii for several decades. Recently many growers in Puerto Rico have begun to recognize the need for control on pineapples and other crops. Cotton farmers in both the Western and Southern States are obtaining higher cotton yields at reduced unit-production cost by using nematocides. In the Southeastern United States nematocides are being used to control several species of nematodes attacking peanuts. Within the past few years, growers have increased their efforts to reduce nematode losses on vegetables, melons, strawberries, grapes, citrus, peaches, and cherries by using nematocides. Chemical control has become increasingly important in forest, fruit, nut, and ornamental nurseries throughout the United States. An interesting new development is the use of postplanting nematocide treatments for partial rehabilitation of nematode-damaged shrubs, trees, and turf grasses, for both home and commercial establishments. However, at present this type of treatment is used only on a small scale.

In the United States nematocides are being used on about 1 million acres of farmland each year, with sales approximating $25 million. Consumer demand for nematocides often exceeds local supplies. The use of nematocides will probably double within the next few years as greater production demands are placed on our farmlands for food and fiber. With the advent of cheaper and more effective means of applying nematocides on large acreage and on moderate acre-value crops, such as corn, cotton, soybeans, peanuts, sugarcane, and forage crops, vastly expanded markets will open. Increased use of nematocides will be necessary because of (1) the trend toward specialized use of land on which crop rotations are not considered practical; (2) increased farm capitalization that requires maximum production, which is impossible without nematode control; (3) greater use of marginal soils, which are frequently sandy and located in warmer areas of the world where conditions are ideal for nematode reproduction and damage; and (4) natural biological adaptations of nematodes that will increase their ability to parasitize and destroy crop plants.

PROPRIETARY NEMATOCIDES

About 20 chemicals and combinations of nematocidal chemicals are manufactured. Many more will be available within the next few years. Those most common and widely used at the present time are volatile, have a fumigating action in the soil, and are referred to as soil fumigants. Some newer nematocides have low volatility and do not diffuse in the soil to any appreciable extent; therefore, dispersal of such chemicals requires good soil incorporation; or they must be moved through the soil by either rainfall or irrigation. Often nematocides are soil disinfestants, and in addition to controlling nematodes they kill soil insects, fungi, and weeds (12).

One of the oldest and widely used soil disinfestants is a mixture of methyl bromide and chloropicrin (Dowfume MC 2). A relatively new formulation of methyl bromide in a petroleum solvent can be chisel injected into the soil with tractor-drawn equipment. Another useful, wide-range soil fumigant is a mixture of methyl bromide, chloropicrin, and propargyl bromide (Trizone). A new and somewhat cheaper soil sterilant mixture is composed of 1,3-dichloropropene and 1,2-dichloropropane and methyl isothiocyanate (Vorlex). A similar mixture of D-D and chloropicrin (Nemex) has been used successfully in some areas of the Western States. Other available commercial soil sterilants include sodium methyldithiocarbamate (Vapam) and 3,5-dimethyltetrahydro-1,3-5, 2H-thiadiazinethione (Mylone).

Most volatile soil fumigants control nematodes primarily, though some may also control certain insects, weeds, and soil fungi. Older chemicals of this type are ethylene dibromide (Dowfume W-85), a mixture of 1,3-dichloropropene and 1,2-dichloropropane (D,D), and a related chemical composed of technical 1,3-dichloropropane (Telone). A highly effective mixture of ethylene dibromide and 1,3-dichloropropene (Dorlone) has proven useful for controlling a wide range of nematode types. Another chlorinated hydrocarbon nematocide, 1,2-dibromo-3-chloropropane (Nemagon), has won wide acceptance because it can be applied to tolerant crops as a preplanting or postplanting treatment in irrigation water in the West and as a granular formulation mixed with fertilizer in other areas of the country.

Within the last 2 years a new, relatively cheap, and low-volume nematocide has been recommended for treating some crops. This chemical, tetrachlorothiophene (Penphene), is particularly interesting because of its similarity to the toxic chemical that has been isolated from marigold roots, which make them resistant to nematode attack (23, 26).

A new chemical, 2,4-dichlorophenyl methanesulfonate (SD-7727), entirely different in nematocidal structure from most proprietary nematocides, has very low volatility and is somewhat residual, with some indication of systemic activity. It appears to be specific for controlling root-knot nematodes, but has little effect on other nematodes found in the soil (14).

ORGANOPHOSPHATE NEMATOCIDES

Many new nematocides currently being developed by industry can be classed as either carbamates (e.g., Vapam) or organophosphates. The organic phosphate group has a greater number of potential new nematocides than the carbamate group. The first organophosphate nematocide marketed (6) was O,2,4-dichlorophenyl, O,O-diethyl phosphorothioate (V-C 13). The second organophosphate (13) of importance as a nematocide was O,O-diethyl O-2-pyrazinyl phosphorothioate (Cynem). A more recent experimental organophosphate is phenyl N,N-dimethyl phosphorodiamidate (Nellite), which is effective only against root-knot nematodes, and may be applied at low dosage in irrigation and transplant water (25). Another experimental organic phosphate nematocide is O,O-diethyl O-p-(methylsulfinyl) phenyl phosphoroathioate (Bayer 25141), which appears to be effective in controlling nematodes in living roots, such as are found in infected nursery rootstock (2, 24). These compounds control many soil insects when applied to the soil at nematocidal dosages, which is usually two to four times higher than those required for economical insect control.

Recent investigations (5, 10, 11, 19) have shown that the following organophosphate insecticides will control nematodes under certain conditions: O,O-diethyl O-p-nitrophenylthiophosphate (Parathion), O,O-diethyl S (and O)-2-(ethylthio)ethyl phosphorothioate (Systox), diethyl-S (ethyl thiomethyl) phosphorothioate (Thimet), O,O-diethyl S-2-(ethylthio) ethyl phosphorodithioate (Di-Syston), O,O-diethyl O-(2-isopropyl-4-methyl-6-tyrimidinyl) phosphorothioate (Diazinon), and O,O-dimethyl S-(methylcarbamoylmethyl) phosphorodithioate (Dimethoate, Cygon). The herbicide Zytron (O-(2,4-dichlorophenyl)-O-methyl isopropyl phosphoramidethioate) has also been found to possess limited nematocidal properties. None of these chemicals are currently recommended for nematode control.

With continued chemical synthesis and improvement of application methods, the organic phosphates probably can be developed into highly effective chemicals for controlling nematodes on established plants, such as ornamentals, shade trees, bulbs, and forage and lawn grasses.

ADVANCES IN NEMATOCIDE APPLICATION

During the past 10 years great advances have been made in developing equipment and improving chemical formulations so that nematode control is now possible for most crop and soil conditions. Recent equipment and formulation advances have made possible chisel application of methyl bromide with tractor-drawn equipment (21, 22), resulting in a saving of time and labor, as well as in the amount of chemical used. New equipment and methods also have been developed for applying general soil disinfestants by in-the-row methods. These improved row-application techniques provide a sterile planting band, or zone, 10 to 14 inches wide in which nematodes, soil diseases, weeds, and insects are controlled. This type of high-level crop protection may be particularly useful in the production of truck crops, which are not of high enough value to justify conventional overall application of general soil disinfestants.

Furrow application of pesticides during the planting operation is becoming increasingly popular (3, 4). Savings in operational cost usually offset losses of effectiveness of pesticides applied in this manner. Nematodes, soil fungi, and insects have been controlled in experimental tests and farm demonstrations by furrow applications of combination mixtures of nematocides, fungicides, and insecticides. Granular formulations, particularly of nematocides containing dibromochloropropane that can be mixed with fertilizers and applied in the furrow, have made control of nematodes practical on a number of relatively low-value crops, such as cotton, peanuts, and some vegetables in several areas of the country.

Recent investigations of nematologists in Arizona and California have shown that some nematocides can be applied in irrigation water (open ditch and flood irrigation) for such crops as cotton, sugarbeets, citrus, and vineyards (16, 18, 20). Nematode control by this method, though not recommended for all crops, usually equals that obtained by more conventional methods. Unproductive groves and vineyards that were in a state of decline caused by nematodes have been restored to high production by this inexpensive method.

RESEARCH NEEDS

Such progress indicates the need of additional research to improve formulations, equipment, and application techniques in order to develop more efficient and economical application of nematocides. Especially needed are techniques to prevent rapid increase of nematodes after chemical treatment, because nematocides seldom rid the soil of these pests, but only reduce their numbers below detection level. Proper soil management after use of nematocides may provide means to delay the return of damaging infestations and thereby reduce the frequency of nematocide use and lessen long-range crop losses caused by nematodes. In addition, basic studies are needed to determine the direct and indirect effects of nematocides on soil organisms and on the soil ecosystem. Such knowledge would provide the basis for manipulating soil and crop management practices for the best possible growth of plants after use of nematocides.

Emphasis should be placed on understanding and developing methods of counteracting the deleterious side effects of nematocide treatment of the soil. The most pronounced of these are nitrification lag, phosphorus deficiency, increased incidence of certain plant diseases, and stimulation of weed growth. Much information is needed on the exact method of nematocide movement in the soil and on the precise manner in which various types of nematocides kill nematodes. We must know whether these materials are adsorbed on or leached from soil, degraded by microbiological processes, or absorbed and translocated by plants. In addition, realistic research programs must be continued to insure that food and fibers are free of harmful nematocide residues, unpalatable flavors, or poor quality.

There is increasing evidence that when nematode damage to crop roots is eliminated, the amount of fertilizer applied to many crops can be reduced, and possible adjustments of the ratio of N, P, and K in fertilizer may be required. Also, trace element deficiencies in plants can be at least partially corrected by controlling nematodes, because a sufficient amount of trace elements may be mineralized in most soils to support normal plant growth, provided root systems are not debilitated by nematodes. Therefore, it is not unreasonable to think that fertilizer recommendations eventually may have to be reevaluated in order to satisfy the nutritional needs of plants with nonnematized root systems. In addition, several exploratory-type investigations have established that modern irrigation practices may increase nematode infestations and that plants with nematode-damaged roots have different water-utilization relations than healthy plants. Such findings indicate that additional research should be undertaken to evaluate the effect of nematocides on the use of irrigation, fertilizers, seeding rates, and other management practices after the soil has been freed of nematodes.

Increased mechanization and interest of growers in reducing the operational costs of applying pesticides may require a single, combined application of agricultural chemicals. A few experiments have indicated that multiple pest control is possible either before, at the time of, or after fertilization and seeding. However, there is a need for additional evaluation of integrated soil pesticide programs, in which nematocides, fungicides, herbicides, and insecticides are applied together, or within short intervals, because not all pesticides may be compatible when used together on some crops. Combinations of pesticides will have to be evaluated for each crop under varying soil and climatic conditions.

NEW APPROACHES TO NEMATODE CONTROL

New approaches to chemical control of nematodes must be developed, particularly for controlling nematodes in and around living plants. In order to achieve these objectives, much additional knowledge is needed of the biochemical interactions between the nematode parasite and its plant host. Knowledge of the biochemistry involved in nematode parasitism of plants, which is being pursued at a number of institutions, may provide the basis for discovering new nematocides, such as systemics, repellents, and chemosterilants.

The discovery of effective, practical systemic nematocides appears to be possible. Several chemicals, with at least some nematocidal activity, have controlled nematodes under experimental conditions (1, 7, 8, 11, 15, 17). Maleic hydrazide gives some control of root-knot nematodes when applied to the foliage. Some control of the bentgrass nematode, which causes nematode galling of seedheads, has been achieved by probable systemic activity of the growth-regulating herbicides 3-amino-1,2,4-triazole (Amitrole), 2-2-dichloropropionic acid (Dalapon), and maleic hydrazide when the chemicals were sprayed on the grass foliage before heading.

Availability of commercial systemic nematocides will often eliminate many of the present difficulties experienced in fumigating soil. Application of systemic nematocides should be relatively simple, and they can be applied directly to the plant or to the soil near plant roots, which can take up the chemical. Systemic nematocides may reduce the need for present soil-fumigation treatments, because the plant itself will disperse the nematocide in soil.

Other profitable areas for research, yet to be thoroughly investigated, are repellents, attractants, and resistance inducers. The action of a repellent should be to disorient the nematode by disrupting the normal detection processes used for finding plant roots. Such chemicals may be applied to plant foliage, to seed as a preplant treatment, or to soil around plants.

The prospect of finding nematode attractants is particularly interesting, because the availability of an effective attractant would provide many possibilities of selecting nematocidal chemicals to combine with an attractant. When properly applied, such a mixture should entice and then kill the nematodes. Successful control of nematodes by this method will require thorough soil incorporation of chemicals, because most nematodes move only a few inches a month, necessitating placement of the chemical near the nematode by mechanical means. This is a difficult problem but not insurmountable with adaptations of modern farming implements.

Current basic studies are providing knowledge of the chemical nature of nematode resistance in plants. It is believed that basic discoveries will uncover chemical structures that may be synthesized and applied to plants so as to induce nematode resistance artificially in plants. This intriguing approach to chemical control offers prospects of rendering common plant varieties resistant to nematodes, and may eliminate the prolonged research required to develop nematode-resistant crop varieties by present breeding methods.

Development of chemosterilants is another possible approach to controlling nematodes. Preliminary investigations by U.S. Agricultural Research Service nematologists and chemists (9) have shown that some highly reactive materials containing aziridine or triazine configurations, such as triethylenemelamine, simazine, and atrazine, and others, such as 5-flurorouracil, are effective in reducing nematode populations under controlled conditions in the laboratory. This work is of basic interest because it is the first demonstration of chemosterilant control of nematodes. These chemicals cause degenerative changes in nematode gonad tissue, especially ovaries, and thereby control nematodes indirectly by reducing the reproductive potential of the nematode population after each reproductive cycle. However, the development of effective, practical chemosterilant methods for nematode control will be difficult, because many of these materials create possible residues as well as mammalian and plant toxicity problems.

From the practical viewpoint, chemosterilants may not prove so effective against nematodes as against insects. The so-called sterile male technique, used so successfully against insects, may be of little or no value against nematodes, because males are not required for reproduction of many nematode species. Also, much of this method's success in insect control depends on a high rate of insect mobility, which allows treated individuals to come in contact with individuals from the natural population; however, as we noted, nematodes move only several inches per month, precluding frequent contact of sterile and normal individuals, which is needed for effective control.

These are but a few of the great advances and problems in the chemical control of plant-parasitic nematodes. Techniques have been perfected, or are in the process of development, for control of many nematode types under a wide range of soil, crop, and cultural conditions. Even greater progress can be expected in the future as new nematocides, disinfestants, and other types of chemicals become available.

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PEST CONTROL BY BIOLOGICAL MEANS

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Unilateral approaches to pest control are yielding to broad, multidisciplinary attacks on noxious organisms. Changing attitudes are an obvious concomitance, and as a result many concepts that were merely abstract ideas only a few years ago are now being put to field tests in an ingenious and imaginative fashion. The once limited and restricted horizons have been broadened tremendously, and this has brought about a situation that is exciting and challenging to biological scientists engaged in the suppression of pest organisms.

These accelerated changes have been particularly impressive in the areas of research dealing with pest control by biological means. The enthusiasm and support for more work on the nonchemical aspects of pest control are unprecedented, and this has two major and immediate benefits: (1) It makes a better balanced research program and (2) it encourages the development of integrated control techniques.

The unmistakable trend is toward the development of broadly based control programs with a definite ecological orientation. Perhaps this was always inevitable. Certainly it is understandable, because pest control is basically achieved by simply creating an environment unsuitable for the survival or increase of the pest. The really significant thing now is that more and more attention is being given to the biotic aspects of this environment. As a result, there is an increasing awareness of the tremendous potential of using biological phenomena in pest control.

There are numerous, convincing, and well-documented demonstrations of the suppression of arthropod pests by purposely introduced parasites and predators. This is the now familiar procedure that we recognize as biological control. Its basic principles were extended to use phytophagous insects for the spectacular control of weeds in Australia, Hawaii, and California. Another logical extension has been the widespread use of pathogens to reduce populations of insects and certain vertebrates through the technique known as microbial control. These examples of applied ecology have now become a familiar part of our pest-control concepts, and are easily caught in the scholastic net of acceptable definitions of biological control.

Although not so easily included in the definition of biological control, there are nevertheless other outstanding advancements that utilize biological phenomena to control pest organisms and that are undeniably examples of pest control by biological means. Among these achievements are the use of resistant varieties of crop plants, the application of the phenomenon of antagonism as a plant disease-control tactic, and the fascinating "autocidal" innovations, particularly the dramatic application of the male sterility principle.

The contributions to this symposium give us an exciting view of the future of pest control by biological means. They also reveal that this area of pest control, with its tremendous potential, has scarcely been explored and should be fully exploited in the future.

PROBLEMS ASSOCIATED WITH THE DEVELOPMENT AND USE OF PEST-CONTROL MEASURES

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One of the simpler views of life holds that problems really aren't as complicated as the experts make them out to be . . . and that difficulties can be resolved fairly quickly and easily if only the experts do what seems obvious to everyone else.

How pleasant it would be if we could so lightly view the crushing responsibilities of the 20th century . . . how reassuring to see the answers to its subtle and defiant problems so clearly and confidently stated.

But how much more difficult it is to have to face up to the unpleasant realities of providing meaningful and lasting answers--whether in the field of international relations, or automation, or pesticides. How much more trying to have to juggle a whole host of potentially lethal weapons, so to speak, while at the same time balancing on a tightrope and being urged to proceed in both directions at the same time--as is happening now in the field of pesticides. The predicament that we find ourselves in today is simply this:

We cannot live without pesticides in this intensely developed manmade society of ours. We could not maintain our agriculture, our health, or our present high levels of comfort and living. But, we are finding it increasingly difficult to live with pesticides.

No thoughtful person today seriously questions the need for pest control in order to maintain a healthy and progressive society. But beyond that, there is a vast amount of public confusion and misunderstanding and even apprehension concerning the aims, techniques, hazards, and even the benefits of pest control.

I suspect that most people, for example, are not aware of the extent of environmental control that is exercised by an orderly society. The better developed nations routinely and continuously modify, adapt, and contain their environments to their own living . . . and the measure of their success is the measure of their development.

I am always amused, and sometimes appalled, at the suggestions made by well-meaning and supposedly knowledgeable biological scientists that we must have as a first objective in pest-control programs the maintaining of a so-called "biological balance" in nature. I know of no highly developed nation at the present time or in the past wherein this biological balance has not been tipped in favor of man and of the plants and animals he consumes.

If man is to enjoy a level of living comparable to that we in developed nations enjoy, he must modify his environment to favor himself. He must use nature's tendency to bring about balance among organisms whenever it helps him control pests. He must combat this tendency when it works against pest control.

Many people are not aware of the extraordinary contributions of pest control to the agricultural revolution that has taken place in North America . . . a revolution that has brought forth such a tremendous abundance of food . . . a revolution that other less developed nations are earnestly striving to bring about in their own lands.

One need not be a historian or a scientist to recognize that lack of pest control has been and still is a serious drawback to national development in many parts of the world.

And I am sure that very few people are aware of the concern of the U.S. Department of Agriculture and its partners in the States for safety in using pesticides. The fact is we do everything we can to insure that pest-control measures are used safely, with minimum hazard to man and animals and the environment. We are, after all, dealing with mechanisms that can affect forms of life other than the ones we are trying to destroy. Safety always has been--and always will be--a major consideration in the development and use of pest-control measures.

Let's turn and look at how far we have come in terms of pest-control measures that are in use today . . . and those that are on the horizon.

Chemical pesticides are still essential to American agriculture and will be for some time. Industry and State and Federal agencies have developed dozens of effective pesticides along with good application techniques and equipment. There are very few pests that cannot be controlled by some kind of chemical compound. We should not for one moment give the impression that, because of some problems associated with their use, we are abandoning pesticides. Because they are effective and relatively inexpensive, we shall continue to depend on these most important chemicals to help us provide an abundance of high-quality food at the lowest prices ever known, when measured in terms of the only true cost, how long we have to work to pay for it.

Today, however, the emphasis of your program is on approaches that do not involve pesticides. There are many of these approaches . . . they are varied . . . some are old and are being looked at again in the light of new information . . . some are new and have unusual interest and merit. May I use as my primary examples, nonpesticidal methods of controlling insects. Similar examples could be cited for control of weeds and plant and animal diseases.

A whole new concept of insect control has opened up with the development and use of the sterile male technique. This method was used a few years ago to rid the southeastern part of the United States of the screw-worm, a serious pest of livestock and wildlife. It is now being used to get rid of the same pest in Texas and New Mexico, and, for all practical purposes, the job has been done. However, screw-worms can and do migrate from nearby Mexico. Thus, we are continuing the program in the Southwest to prevent reinfestation.

In both program, the insects were sterilized by exposing them to gamma radiation from a radioactive cobalt source. More recently, we have made good progress in finding chemicals that will sterilize insects without otherwise affecting their behavior. House flies, mosquitoes, and boll weevils have been safely and effectively sterilized. We're already using chemosterilants to control the Mexican fruit fly population on the California-Mexico border. We hope to devise techniques for placing chemosterilants within reach of some of our most important insects. They would, in effect, treat themselves.

The sterile male technique for controlling pests--using irradiation or chemosterilants--does not represent a widespread weapon at the present time. But as we work out better ways to use the technique alone or in combination with others, we believe it will become a major and highly effective weapon in the future. Chemosterilants, particularly, will be more widely utilized, we feel, as we develop and use attractants as a means of exposing insects to these chemical compounds.

The use of natural and synthetic insect attractants offers almost unlimited opportunities for controlling pests. This is not a particularly new approach. We've worked with attractants of one kind or another for many years. Their heightened appeal at this time lies in the fact that we are finding some new and highly active attractants, and are improving our techniques for using and evaluating them.

We've recently developed protein hydrolysate bait sprays for tropical fruit flies; granular and other baits for house flies; mirex with bait for fire ants. And, in one of the outstanding recent achievements of entomology research, we eradicated the Oriental fruit fly from the Pacific island of Rota by using a sex attractant--which drew the insects from a considerable distance--along with an insecticide--which actually killed them. Mechanical traps, pathogens, or sterilants are equally effective in destroying pests in this situation.

Certain kinds of light show promise in controlling insects, particularly those that fly long distances, such as some of the tobacco, cotton, and cabbage pests. We trapped tobacco hornworms in an area of 113 square miles in North Carolina for 3 years in succession, using near ultraviolet light. By so doing, we reduced the population of this pest by 90 percent. The use of light was coupled with the destruction of tobacco stalks late in the fall.

We have been able to utilize other forms of light as well as sound and radio waves to control insects on an experimental basis. We found that the larvae of certain insects are interrupted in their development when they are subjected to flashes of light, even as small as 1/1000th of a second. We have experimented with radiofrequency electromagnetic fields in controlling grain insects . . . and feel this is a promising technique.

Another highly desirable and economical non-chemical approach is to breed plants that are resistant to certain diseases and other pests. There's a great deal we can do to fully exploit this practical approach. Research resources in the past have rarely been adequate to take on both the short-term work needed to solve immediate problems and the long-range exploration needed to develop this technique.

Yet, in instances where a concerted research effort was made, we've been able to develop varieties resistant to disease and insect attack. The development of wilt-resistant alfalfa varieties and others that resist the spotted alfalfa aphid is an outstanding example. Good progress has been made in breeding corn hybrids resistant to diseases, such as smut and stalk rot, and to insects such as the European corn borer. We have sugarbeets resistant to curly top, potatoes that resist leaf roll, and numerous varieties of winter wheats resistant to various strains of rust and to insects such as the Hessian fly. Plant breeding along with pesticides has contributed to a reduction in damage from nematodes--one of our most devastating pests.

It is interesting to note that Australians have reported cattle strains that appear to resist the cattle fever tick.

I believe we will continue to find satisfactory solutions to many of our problems in future years by breeding crops and animals that resist attack by some of their most destructive pests.

In addition to plant and animal breeding, other biological methods for controlling pests are among our most important approaches, although not at the moment among our most extensive practices. The activities of biological control organisms in nature are extremely beneficial. But, when these organisms are used for specific control purposes, they often are not adequate to meet the standards of agricultural production efficiency our modern economy requires.

Yet we know that their use in the years ahead will likely increase substantially . . . and their development remains only to be fully explored and exploited. These natural control techniques include natural enemies of insects and weeds, such as parasites and predators; pathogens, such as bacteria, fungi, protozoa, and viruses; alteration of genetic characteristics of the pest; and preventing seed or pollen production of the unwanted plant.

The potential use of one organism to control another is unusually promising. We already have several such organisms for a few pests--the milky spore disease to control the Japanese beetle; the *Bacillus thuringiensis*, which controls several insects. These organisms--which can be applied directly to crops in the same way as insecticides--appear to be specific in their action, and they do not impair the work of parasites and predators.

We are continually finding new insect pathogens. And we are making excellent progress in developing techniques for the mass production of specific organisms for practical use.

Only recently we found two virulent protozoan organisms that may provide a safe and effective way to control the boll weevil--a pest we have been investigating for over 60 years.

Just as insects are attacked by other organisms, they in turn can be used to eliminate other insects and unwanted plants. The U.S. Department of Agriculture has brought in about 650 natural enemies of insects and weeds since 1888, and about 100 of them have become established. Perhaps the best example is the use of beetles to control Klamath weed, a destructive pest in the western part of the United States. I am told that 2 million acres of this weed were destroyed by this unusual method. We are continuing the worldwide search for these parasites and predators and believe they will always be an essential part of our pest-control practices.

Cultural and management practices that reduce the necessity for pesticides have long been successful and are constantly being improved. Such practices as crop rotation, balanced fertilization, plowing under and burning stubble, destruction of insect breeding places, and adjustment of planting and harvesting dates to minimize pest damage all have their place in controlling pests. Sanitation practices and management systems to break the life cycles of internal parasites keep some livestock diseases in check without pesticides.

So, as you see, we have a large arsenal of weapons at our disposal, and many of them can be combined in various ways to do an even more effective job. But we do face some rather formidable *obstacles* in *developing* these measures to their fullest possible potential. May I cite a few of these obstacles.

First, we simply don't know enough about the pests we are dealing with and trying to control, whether by chemical or nonchemical means. Their life cycles, physiology, ecology, genetics, and growth habits are still largely mysteries that we are just beginning to unravel through strong basic research.

This information is important in developing chemical means of pest control. It is absolutely essential if we are to supplement chemical control with biological means. We are attempting to control weeds and insects for example, whose life cycles are completely unknown. We don't know for certain whether some weeds are perennials or annuals. Such knowledge is essential if we are to develop the best means of eliminating these pests.

Second, we cannot predict with any certainty the effects of various kinds of treatment on the pests we are trying to control . . . or on the other organisms in the environment. This is equally true of biological materials as well as chemicals. This results from inadequate research on the pests themselves and forces us to use "trial and error" methods in using pesticides, rather than methods based on knowledge of the pests and their life processes.

Third, we know too little about the fate of chemical compounds as they move from the target area to other segments of the environment. We have inadequate knowledge of their movement in the atmosphere, into and through soils and into our streams, rivers, and oceans. There is a great void in our knowledge of the breakdown of pesticides in soils, plants, and water--and of the intermediates formed from this breakdown. Until this kind of information is available, we shall be living under a dark cloud of doubt as to the complete harmlessness of chemical pesticides.

Fourth, we are handicapped by our lack of knowledge of the extent of buildup of toxic quantities of pesticides in the food chain--and of the mechanism of this buildup. Such knowledge would help identify potential nontarget hazards of pesticide usage and would assist in the diagnosis of alleged adverse effects of pesticides on fish and wildlife.

Fifth, we need more information on the toxicity of pesticides to fish, wildlife and other animals. This would provide guidelines for restrictive use where potential hazards may exist.

Last, but certainly not least, we need additional scientific manpower trained in select disciplines of the physical and biological sciences to carry out the new lines of research. The background of these men will differ from that of their predecessors. There will be a higher proportion of organic chemists, biochemists, geneticists, physiologists, ecologists, and climatologists--men with specific training to carry out specific assignments. Some new scientists are being supplied through expanded graduate training programs in our universities--the research component of which is supported at least in part by USDA grants or contracts. Others will come through the retraining or updated training of scientists within the department. Both the training and retraining programs will need to be stepped up drastically.

The problems I have mentioned in developing pest-control measures are essentially the same ones we face in using these measures.

In using chemicals, our greatest difficulties stem from the fact that some of them tend to persist in the environment, that is they are biologically nondegradable. This fact is significant since the use of persistent chemicals places in our environment compounds we cannot destroy. An even greater problem, however, is the fact that they may become widely disseminated as residues in soil and water and build up in the bodies of biological organisms used for food. Although we believe our food supply is safe at the present time, we are alert to the possibility of a pesticide buildup in the food chain and want to do all we can to prevent it.

The only effective solution is to develop highly selective pesticides that can be applied precisely to kill only the pest we want destroyed--not anything else--and that persist just long enough to do the job. Pesticides that approach this ideal are on the market and their number is growing.

In some cases, of course, persistence is desirable and assures effective destruction of some pests. When such compounds must be used because nothing else will do the job, obviously, we must use them but with the greatest possible caution.

Another difficulty we face in using pesticides is related to the phenomenal expansion of their use in our modern society. Some pesticides are used today in quantities 100-fold or even 1,000-fold greater than those used in 1950 and in locations and for specific uses that were not even recorded in the statistics of that year. It is only natural that difficulties arising from misuse or from movement to nontarget areas are more likely to occur today than 15 years ago.

An omnipresent problem in the use of pesticides is the development of resistance by the pests to the chemicals. It is sometimes a race to find a new control method, chemical or otherwise, in time to take the place of the chemical to which the pest has developed resistance.

Perhaps the most significant practical obstacle is the misuse and improper use of chemicals. In spite of valiant educational efforts by industry and public agencies, chemicals are sometimes misused. One mishap, especially if not detected, can bring about serious damage to nontarget organisms--thus opening to criticism the many who carefully observe the safety precautions.

In using biological control methods, we may have some difficulties similar to those associated with chemicals. We will have to be certain that the agents we select--parasites, predators, or pathogens--will attack only the pests we want to destroy. There is the possibility that the pests may also develop resistance to the natural organisms we use for control purposes. There is also the possibility of misuse or improper use.

One of the major difficulties is that it costs so much to develop biological control techniques . . . and it takes so much time. There are thousands of pests in every conceivable environment. All of them prey on man or his plants or animals. All of them have different habits and metabolic behavior. All of them resist our best efforts to control them. Each one requires individual exhaustive study--a truly monumental effort. Research costs to develop biological means of control will likely be several times those for chemical means--and we know the relatively high costs of the latter. We have already taken the first few steps with the recent launching of a greatly intensified program of research and education on pesticides.

This program--one of the strongest in Department history--will enable us to do the basic and applied work that has long been necessary. The State agricultural experiment stations will cooperate in this stepped-up effort. That cooperation will continue, as both of us are seeking the same end--the safest and most effective pest-control methods that human ingenuity can devise. And, as always, we will have the cooperation and assistance of the chemical industry.

Joint effort in entomology, by the way, is not limited to the United States. The Department of Agriculture has been fortunate in sharing the closest working relationships with scientists here in Canada, especially on studies dealing with biological control techniques. We look forward to enjoying a continuation of that excellent relationship.

May I list briefly the major features of the expanded program, since it may help alleviate some of the difficulties I outlined in the earlier part of this paper:

(1) Basic research on the pests themselves, their life cycles, growth habits, physiology, ecology, genetics, etc.

(2) Basic and applied research on biological methods of control.

(3) Research to refine and improve chemical methods of control designed to decrease the chances of polluting nontarget areas of our environment.

(4) Research on the fate of pesticides and on their toxicity to farm animals.

(5) Economics research to identify the true economic importance of pest control.

(6) Improvement in regulatory and control procedures, including the monitoring of agricultural areas for pesticides.

(7) An expanded library service to provide scientists and educators in all fields with a monthly digest of current research and development programs dealing with pesticides.

(8) An expanded extension education program to train people in proper handling of pesticides. These programs are being developed for homemakers who use pesticides in their homes, gardens, and lawns. Special training sessions are being set up to instruct farmers, commercial spray operators, and personnel in the pesticide industry on the proper way to handle pesticides. We will be trying to reach everyone--city people as well as farm people. We want to get across two ideas: (1) Effective pest control is essential if we are to maintain our high standard of living and if this abundance of quality food and relative freedom from the hazards of pests are to be enjoyed by all mankind; and (2) pesticides must be used safely, in the same way as medicines, atomic energy, or any of the other modern techniques that make this a more satisfying world.

There is no mistaking the work that has been cut out for us in the field of pest-control studies. The challenge is clear. It is not going to be answered quickly. There may not be any "final solutions." Nature is dynamic, changing, and fluid in its manifestations. Our methods for dealing with pests will have to go nature one better. We will have to anticipate its intricate movements, and be prepared to handle situations as the need arises.

We will not, like the scientists in Jonathan Swift's famous fictional Academy of Ladago, be concerned with brilliant inventiveness on wildly impractical things--like building houses from the roof downward to the foundations, or extracting sunbeams from cucumbers and sealing the beams in bottles to warm the air on cold and rainy days. Science in Swift's fictional country is brilliantly and wastefully preoccupied with esoteric problems while the country lies destitute and in ruins. Our aim in the pest-control studies, as in all our work, is directed toward the improvement of man's lot in life.

Our somewhat more humanistic approach to science has brought us rewards beyond measure. But there's no law of nature that says we automatically and rightfully will continue to be so rewarded--not without great effort and cost. No one knows this better than the scientists involved in the daily business of wresting knowledge from an unconcerned and unyielding nature.

As we understand the biology, ecology, and behavior of insects . . . and the proper integration of several methods of control . . . I believe we will see, in our own lifetimes, the basis laid for practical, nontoxic, and effective methods for dealing with pests.

PRESENT AND FUTURE ROLE OF PARASITES AND PREDATORS FOR INSECT CONTROL

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Parasites and predators have a vast potential for use in pest control, but this potential remains largely unexploited. Whether or not it will be adequately exploited in time to meet the needs of the future is debatable.

Control of a pest insect, or, to be more accurate, control of the harm that the insect causes to man and his property, involves manipulating the environment to reduce or remove factors that are favorable to the pest or to add or increase factors that are unfavorable to it.

Parasites and predators are among the factors that are unfavorable to pests. They are unfavorable, and thus beneficial from our viewpoint, because they, like chemical pesticides, kill the pests. However, unlike chemical pesticides, they are already present in the environment, as virtually every insect is attacked by parasites and predators under natural conditions.

Therefore, because they already exist, parasites and predators may be manipulated for pest-damage control in ways that are additional to adding them to an environment where they did not occur previously. In fact, they can be manipulated, directly or indirectly, in four main ways:

First, by removing from the environment, or otherwise reducing the effects of, factors that kill parasites and predators, prevent them from increasing, or restrict their activities;

Second, by adding or increasing environmental factors that are favorable to the multiplication or activities of parasites and predators;

Third, by increasing the numbers of the kinds of parasites and predators that are already present, by liberating quantities of the same kinds that are obtained by mass-rearing or by special collections;

And fourth, by increasing the various kinds of parasites and predators by liberating new kinds imported from elsewhere.

All these ways are feasible. All have been shown to be effective pest-control methods. None has been used in more than a small fraction of the pest situations in which it might be effective.

An example of the first way that is unusual because it is applied in many countries is the protection of insectivorous birds from destruction by man. A better example of factors that are harmful to parasites and predators and that can be manipulated to decrease this harm is chemical pesticides. In both these examples man's activities are the harmful factors.

It is now generally recognized that chemical pesticides are commonly misused, and that they often tend to intensify existing pest problems and to create new ones by destroying the parasites and predators that were--before the chemicals were applied--important in keeping the pest from increasing unchecked.

Integrated control programs can overcome this problem.

Integrated controls are control measures applied in such a way that their effects do not counteract either one another or the effects of naturally existing factors that regulate pest numbers. In its simplest form, an integrated control is the use of chemical pesticides in such a manner that they do little or no harm to the parasites and predators that attack the pest. More usually, integrated controls involve manipulating, in addition, parasites, predators, and other controls.

The rate at which an optimum integrated control program can be developed for any pest situation depends on the rate at which knowledge is obtained on the identities, life histories, habits, and ecology of the parasites, predators, and other natural enemies of the pest. When we have such information, we can both manipulate the natural enemies of the pest to increase their effectiveness and at the same time plan modifications of chemical treatments on a basis of facts, so that the chemicals will have little or no effects on the natural enemies.

Unfortunately existing knowledge is often quite inadequate. For example, in Canada there are about 2,000 kinds of insects that are harmful to agriculture. But some information on the identities of their parasites and predators is available for only under one-third of them, and in only a few instances is the information sufficiently adequate to form a basis on which optimum integrated control programs might be developed. When you consider this situation in the context of the fact that insect pests have been studied in Canada as intensively as in any country and more intensely than in most, you will appreciate how much remains to be done everywhere. Good integrated control programs have been developed, for example, that for the spotted alfalfa aphid in the Western United States, but they are still exceptions rather than the rule.

However, it is possible to develop rather effective integrated control programs on a basis of probabilities. These probabilities, which are in practice virtual certainties, are that parasites and predators that attack the pest are present, they are not always where the pest is, and when they are where the pest is they are liable to be killed by chemical pesticides. Therefore, chemical applications that are reduced to the minimum in terms of time and quantity will have the minimum of harmful effects on the parasites and predators, which will therefore survive to assist in controlling the pest numbers.

A program of this kind was developed by the Canada Department of Agriculture for fruit tree pests in Nova Scotia, and is widely used by growers in that Province. Similar programs could be developed for other pest situations and in other areas. In most instances, they have yet to be developed, but they doubtless will be.

The second way that I mentioned of manipulating parasites and predators to increase their numbers is to increase environmental factors that are favorable to them. This is a little-used approach but one that has much potential. But again, a knowledge of the ecology and behavior of the parasites and predators involved is an essential prerequisite.

This method is based on the principle that most parasites and predators have essentials for survival and increase that are not provided by the pest itself or its immediate environment. The parasites must go elsewhere to find the alternate hosts on which they complete their annual life cycles, or to find the food that the adult females must have before they lay their eggs. The predators must go elsewhere to find alternative prey on which to build up their numbers or to survive periods when the pests are not available to them. And both parasites and predators may require special hibernation or nesting sites.

In some pest situations in Western Europe, nesting sites are deliberately provided for birds and ants that prey upon the pests. In the Soviet Union, various pests are stated to be kept under satisfactory control by growing with the crop the wild flowers on which the adult parasites must feed before they can lay their eggs on the pest.

In general, the value of this method seems to be better recognized in Europe than in North America, though there is a classic example, apparently still unpublished, of the control of a grape pest in California by conserving the alternate host that was essential to the survival and increase of the parasite that produced the control. However, this is only one of the few possibilities that have been exploited among, probably, many thousands that have yet to be explored.

The third approach, the liberation of quantities of parasites or predators of kinds that are already present, also is used with success in a few situations. Trichogrammid egg parasites of various pests and ladybug beetles that prey upon aphids, mealybugs, and scale insects are sold commercially for this purpose. In general, though, relatively more attention seems to be given to this approach in the Soviet Union and China than in North America, perhaps because of a relative scarcity of chemical pesticides there combined with greater control over what is believed to be best for the growers.

The difficulty in using living insecticides of such kinds is that it is usually difficult to produce them at economic cost. The problem is that they have to be reared on living insects that themselves have to be reared. The widespread use of parasites and predators as living insecticides awaits the development of artificial diets on which they can be mass-produced at low cost in the quantities and at the time that they are needed.

I now come to the fourth main way of manipulating parasites and predators--by adding new kinds imported from elsewhere. This is of course what most people think of when they hear the term "biological control," though in fact that term covers a much wider range of procedures, including, among various others, those that I have referred to already.

This pest-control method has a unique advantage, which arises from the fact that the control agents, the parasites or predators, are living organisms. This advantage is that the control is self-perpetuating. Parasites or predators not only can reduce a pest population but also can keep it down permanently without further human assistance. The result is that the pest ceases to be a pest or becomes one of relatively minor significance. Obviously to make a pest insect a nonpest is far better than to have to apply temporarily effective controls regularly.

Various pests in many countries have been brought under control in this way. To take Canada as an example, there are over a dozen former pests that are now of less or no economic importance because they are permanently controlled by parasites or predators originally imported from abroad and established here. They include, for instance, the wheatstem sawfly in Ontario (though not in the Prairies), the woolly apple aphid, the oystershell scale, the apple mealybug in British Columbia, and the larch casebearer in Ontario.

The potential of this control method is by no means exhausted anywhere. Again I will take Canada as an example. Including forest insects, we probably have about 3,000 species of insects that can cause economic harm. Probably several hundred of them have the status of permanent pests that regularly cause sufficient harm to warrant control measures. Control with imported parasites or predators, that is, self-perpetuating, permanent control, has been attempted against up to 35 of them, or little more than 1 percent of the total and under 10 percent of the significant pests. So far as I can estimate, the corresponding proportions for the United States, Australia, and other countries where this method has been widely applied are similar. Though many pests are not amenable to control in this way, it is nevertheless apparent that many possibilities remain to be explored.

A reason for increasing the role of parasites and predators in control programs is that they lack those disadvantages of chemical pesticides that have caused so much informed and misinformed comment in recent years:

(1) They are usually specific to the pests that they attack, at least for all practical purposes. This means that they are usually harmless to one another and to other control agents, and consequently, unlike chemicals, do not tend to intensify existing pest problems or to create new ones.

(2) There is no problem whatever with toxic residues; and resistance by pests develops so rarely and slowly, as compared with resistance to chemical pesticides, as to be normally insignificant.

(3) Because they are alive, they are self-perpetuating, self-increasing, and self-dispersing and can continue to produce their control effects indefinitely without continuing human assistance. Moreover, they actively search for the pests that they attack and spread into new areas.

(4) Finally, they are there, waiting to be manipulated and used: they do not have to be invented, developed, or manufactured.

As parasites and predators have all these advantages over chemical pesticides, you may wonder why their demonstrated potential is, as I have shown, by no means adequately exploited.

One of the most important reasons for this arises from a disadvantage of parasites and predators as compared with chemical pesticides: they are usually relatively slow in producing their effects. It may take weeks, months, or years for them to get pest populations under control. Growers prefer something that produces immediate and visible results, as do chemical pesticides, even if those results are only temporary.

A supplementary disadvantage arises from the fact that parasites and predators are alive, and thus to some degree inherently variable in their characteristics and unpredictable in their behavior: a living organism does not always do exactly what another living organism--in this case, man--wants it to do.

The other important reason why parasites and predators are inadequately used in pest control is inadequate information. The grower does not know enough about how they might be used to his advantage because the people who advise him do not know enough about this. They do not know enough because enough is not known. Enough is not known because not enough research is being done. There is not enough research because there are not enough suitably trained people to do it. There are not enough suitably trained people because enough highly trained specialists are not being trained by the universities, and they do not train them because they lack the specialists to do so, and because students tend to gravitate to subjects that receive publicity because they have the money to publicize.

There are, for example, only two universities in the United States, and none in Canada, that have adequately sized departments of biological control. A result is that the demand for specialists far exceeds the supply, and every biological control research center has a problem of staff shortage, which has arisen from the fact that the need for research in the subject has increased faster than an increase in the number of specialists available to do that research.

I have surveyed briefly the present role of parasites and predators on insect control. The other aspect is their future role. The first question that arises is, will parasites and predators be used increasingly? The answer is yes. As I have just indicated, there is already a marked trend in this direction. Evidence of this is that the various existing national and international biological control research agencies have expanded in recent years or are in the process of doing so, and new ones are being established or are planned; and the amount of research, as indicated by the number of research papers published annually, has more than doubled in less than 10 years.

Incidentally I should perhaps mention here that Canada recognized early the importance and potential value of parasites, predators, and other biological controls and developed and supported study of them. As a result, we now give, through the Federal Departments of Agriculture and Forestry, relatively much more attention to research in this subject, and have done so longer than most other countries.

The second question is, will the amount of research increase sufficiently rapidly to meet the needs? There are two main needs. The first is to find effective alternatives to the excessive use of chemical pesticides, because of their toxic and other harmful effects. The second is to develop the optimum control program for each pest situation. As I indicated earlier, most optimum control programs are likely to be integrated controls, in which parasites, predators, and related natural controls are manipulated to make them operate as efficiently as possible and chemical pesticides are applied to supplement these effects without harming them.

Optimum control programs are of course highly desirable at present. A time will come when they will be essential rather than desirable. They will become essential when the increasing world population makes pest control essential: when we will be unable to continue to afford to feed both pests and people. Then it will be essential both to apply control measures and to apply the best ones. A situation may develop where the prevention and control of pest damage cannot be left to the decision and judgment of the individual who is directly affected, as is to a large extent at present.

Something that retards the development of optimum control programs arises from the existing classification of controls into chemical control, biological control, and so on. These are of course useful as descriptive terms for different control methods. The problem is that each method tends to have proponents who give inadequate or no attention to other methods and on occasion oppose and defame them. This retards the development of the best control programs, which must be based on an objective evaluation of all methods in relation to each pest situation, which in turn involves regarding control as a unified concept and not as consisting of a number of more or less mutually exclusive methods.

Many of the people who study and develop controls are employed by industry, and consequently have a commercial motive in promoting particular kinds of controls, notably chemical pesticides. It would thus not be reasonable to expect them to be active in promoting control as a unified concept, other than as a defensive reaction to criticisms.

The appropriate action should come from the nonprofit organizations, such as government agencies and universities. However, at present many of those employed by such organizations also emphasize the study of controls that are based on chemical pesticides and tend to ignore parasites, predators, and other nonchemical controls. A significant reason for this is that those individuals often are under direct or indirect pressure from the public to produce usable results quickly. This influences them to concentrate on the chemicals, which are readily available, have known characteristics, and produce more or less predictable effects, rather than to take the time and trouble to explore and develop the unknown potentials of parasites and predators.

The study of the control of insects that are harmful to man's property is no different in principle from the study of the control of disease organisms that are harmful to man himself. A difference is that pest control is 50 or 100 years behind human medicine. We are still primarily using ways of suppressing the symptoms quickly and temporarily rather than trying to find ways of preventing and curing the ailments. And in control programs we primarily use general-purpose nostrums, and with little regard as to how they may affect the patient's health or length of life or lower his resistance to attack by the same or other ailments.

Modern medical research is aimed primarily at finding ways of preventing disease infection by manipulating the environment, of preventing it from developing if infection does occur, and of curing it as quickly as possible by remedies that best combine maximum effectiveness with minimal harmful reactions, residual effects, or permanent damage. Pest-control research should be primarily directed toward the same objectives. This would involve much greater relative emphasis than exists at present, or than is indicated by existing trends, on the study of parasites, predators, and other nonchemical controls and on their interrelations.

The rate at which this emphasis will increase will depend basically on the attitude of the governmental and university agencies responsible for pest-control research, as on their attitude depends the numbers, the outlook, and the nature of the work of those whom they train and employ. Those agencies would have to take, more than now, the long-term view, as distinct from the short-term view of the grower who tends to be satisfied with measures that ostensibly cure his immediate problems immediately. And they would have to evaluate and compare different control methods objectively, and not be influenced by biased propaganda from industry or uninformed pressure from the public. How quickly those agencies will do this and whether they will do enough soon enough nobody can predict.

A final question is, how extensively will optimum control programs be applied after they have been devised? The reason for this question is that such programs often may be too refined and complex for the grower to apply them himself. The extent to which they will be applied may depend largely on the extent to which experts will be available to apply them. Again, we have a parallel with medicine, where treatment is increasingly by experts rather than by the patient himself or his family.

The future is, as I have suggested, in regarding control as a unified concept and thus in developing programs of integrated control, in which parasites and predators have a far larger role than now. I suggest that the future in the pest-control industry lies more in providing expert services to the public by applying integrated controls than in the sale of chemical pesticides alone.

INSECT PATHOLOGY, PRESENT AND FUTURE

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It was very appropriate that the title proposed for this presentation offered a forward view rather than a backward look at the field of insect pathology. To attempt to rewrite or improve on the reviews and articles of Steinhaus (1956, 1963, 1964), of Poltev (1963), and of Franz (1961) would be to gild the lily. Suffice it to remind you that entomologists in North America have been intrigued by the occurrence of disease in insect populations from the beginning. Natural disease epizootics are very impressive when they affect an insect under study. As a matter of fact, they can put an insect ecologist out of work for a whole season or longer. Consequently, observations of insect disease are scattered throughout the earlier literature.

Contributions by White, Glaser, and others stimulated early interest that culminated in the establishment of a laboratory of insect pathology under E. A. Steinhaus at the University of California in 1945. In 1946, the Canadian Department of Agriculture set up a superb laboratory for basic research in insect pathology in Sault Ste. Marie, Ontario, Canada. Since then, many fine laboratories committed to this field have been built all over the world, and a recent compilation of investigators interested in insect pathology lists more than 400 names.

The emphasis placed on basic research in insect pathology by most of these new laboratories has been most rewarding. In the last 20 years, enormous strides have been made and a large amount of knowledge has been accumulated concerning several groups of micro-organisms that have great potential for insect control. Several men, such as E. A. Steinhaus, J. J. DeGryse, E. F. Knipling, P. Grison, K. Aizawa, and J. Franz, are responsible for encouraging, and sometimes insisting upon, the basic research necessary to understand the principles of microbial control. Thus, it is that insect pathology has developed recently with an excellent balance maintained between the basic and the applied research. The wisdom of this approach, as reflected in the confidence that insect pathologists have in the use of microbes to control some of our insect pests, is now a certainty.

The study of insect micro-organisms has been somewhat biased. For example, study of the protozoa that infect insects has been until recently a rather neglected field. Such neglect might be due to the difficulty in propagating these fastidious organisms or it might be that the protozoa, as a rule, do not create sensational mass epizootics. They do, however, exert enormous pressures on insect populations by retarding larval development in the field and thus expose the target insects to natural enemies longer; and they also reduce the fecundity. These organisms might well be used for long-term, integrated control agents against insects affecting forests, in which time would be of less importance than in field crop protection. Other protozoa, such as some of the schizogregarines, are highly virulent and might be used to great advantage in normal control actions. The works of several scientists are worth studying in connection with these fascinating organisms. They are J. Weiser of Czechoslovakia, John Paul Kramer and R. E. McLaughlin of the United States, J. Lipa of Poland, and Elizabeth U. Canning of England.

The fungi in insect pathology are an enigma. These organisms kill countless insects yearly. Apparently they select their own time and place to do so. Attempts to use these organisms have not been universally successful and, without a doubt, the pathology of entomogenous fungi is one area in which basic research is absolutely essential. Extensive studies on entomogenous fungi have been progressing for some years now under the direction of D. M. MacLeod of Canada, Müller-Kögler of Germany, M. F. Madelin of England, and J. N. Couch in the United States, yet many problems of the most basic nature still exist. For example, the fungi usually invade through the integument; yet our knowledge is negligible of the precise means of invasion, the enzymes used, the optimum conditions for invasion, and the mechanics of this operation.

We are aware that fungi are likely affected by temperature and humidity, yet conflicting reports of the effect of these parameters on insect attack by the organisms leave us helpless to use these agents with knowledge. We are aware that fungi are variable, that they mutate readily; but we know nothing of the relative insecticidal and invasive ability of the strains that are selected by environmental conditions. Here indeed is a rich field of endeavor; and until we obtain more knowledge of this type, we are unable to make full use of these promising agents in microbial control.

The Rickettsiales have until recently been of more concern to medical entomologists than to insect pathologists. These are fastidious organisms that usually have a long developmental period in the host and thus likely are not so useful for rapid, decisive control as some pathogens from other groups. The suspicion that the Rickettsiales isolated from insects may have the ability to grow in animal cells makes them unlikely candidates for general insect control at present. Nevertheless, several investigators, including A. Krieg, A. Huger of Germany, and S. R. Dutky of the United States, continue their investigations of this group.

There are over 100 species of nematodes associated with insects. These animals could be developed into desirable control agents; however, their requirements in the field are just beginning to become understood through research by S. R. Dutky, H. E. Welch in Canada, and J. Weiser in Czechoslovakia. More extensive research in field application and assessment is required along with supporting basic research on nutrition and effect of environment.

The first successful attempt on this continent to use micro-organisms was carried out by Dutky, who used the bacterium Bacillus popilliae Dutky to control the Japanese beetle (Popillia japonica Newman). After intensive basic research on the disease and the disease organisms, Dutky devised a method of producing the organism by using the insect as a living culture medium. Through his efforts the project developed into a massive control program between 1939-52 that was carried on in 14 States and the District of Columbia and involved the distribution of 184,000 pounds of spore-bearing preparation at 140,973 sites on 109,119 acres.[1] One company is still producing the spore preparation according to Dutky's method, while intensive research is being conducted on alternative methods of producing this bacterium by the fermentation process at the Northern Utilization and Development Laboratory at Peoria, Ill.

Dutky gave us more by this classical example of research and development than is first apparent. He delineated the route we must follow in the development of a microbial agent from the original isolation to the application of a competent insect-control preparation. Most of his findings have been summarized in a recent publication (Dutky 1963).

The key Dutky gave us to increased use of insect pathogens, today and in the future, is production of large amounts of the pathogens now available. There are now in existence many fine bacterial, viral, and protozoal pathogens, and most of these grow only in insect tissue. Several of these available micro-organisms have been laboriously produced in gram quantities for limited field trials by Government agencies throughout the world. As a result of these trials, we are certain that the potential of these organisms is enormous; yet no further progress will be made and large-scale use will not be possible until the micro-organisms are produced in sufficient quantity for massive field testing.

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[1] Report of Chief of former U.S. Bureau of Entomology and Plant Quarantine, 1953.

Furthermore, the whole problem of the general use of a microbial agent is not apparent until it is mass-propagated. An excellent example of the problems that arise can be illustrated by the mass-production of the organism Bacillus thuringiensis var. thuringiensis Berliner. About 1956, Bioferm Corporation, Wasco, Calif., pioneered the production of this bacterium and was closely followed by such companies as Nutrilite Products, Inc., Merck Sharp and Dohme, Rohm and Haas, and the Grain Processing Company. The resulting cooperative work among these companies, interested laboratories, and Government laboratories aiding in field testing made available a huge amount of encouraging data concerning the efficacy of this superb control agent. However, a large number of unexpected problems arose from the initial work--problems of fermentation, of proper bioassay, of specificity, of formulation, and so forth. Most of these problems have been solved or their solution is in hand. None of these very important problems would have been solved by this time without mass-production of the organism.

During the past two decades, we have been increasingly aware of the great potential of insect viruses as insect-control agents.

You are probably aware of the following types of insect viruses: (1) Nuclear polyhedroses, (2) cytoplasmic polyhedroses, (3) granuloses, (4) polymorphic inclusion viruses, and (5) noninclusion viruses.

There are, collectively, about 225 species of insect viruses now isolated. Of these, the nuclear polyhedroses (107 species), the granuloses (35 species), and the cytoplasmic polyhedroses (80 species) are the most likely candidates for insect control.

Several of these viruses have been tested in the field. The virus materials for most of these tests were obtained from insects reared on the natural plant at one time during each year when the larvae were available. More detailed information on these methods is available from an article by Martignoni (1964).

Thus, we find that less than 10 percent of the viruses have had field trials. The reason is that production of sufficient virus material was too costly and time consuming for many of the interested Government agencies to attempt.

Fortunately this stage of helplessness in insect pathology is almost over. By their intensive research, entomologists all over the world are amassing valuable information on techniques for rearing many of the economically important pests on artificial or semi-artificial diets, permitting yearround, relatively inexpensive rearing of insects.

If an insect can be reared after this fashion continuously, it is then almost always possible to devise a method of propagating the specific virus of that insect.

Recently Ignoffo (1964) devised methods for producing the nuclear polyhedrosis of the corn earworm [Heliothis zea (Boddie)] (on cotton, the bollworm), that of the tobacco budworm

Table 1.--Insect viruses

Type of virus	Estimated species	Orders affected
	Number	
Nuclear polyhedrosis..................	107	Lepidoptera and Hymenoptera.
Cytoplasmic polyhedrosis...............	80	Lepidoptera.
Granulosis.............................	35	Do.
Polymorphic inclusion virus............	2	Lepidoptera and Diptera.
Noninclusion virus.....................	5	Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Arachnids.
Total..........................	229	--

Table 2.--Major lepidopteran pests that have viruses and can be reared on artificial diets

Species	Authority[1]	Virus	Authority[2]
Beet armyworm (*Spodoptera exigua* (Hübner))	(22)	Nuclear polyhedrosis	(13)
Cabbage looper (*Trichoplusia ni* (Hübner))	(8)	do	(4)
Codling moth (*Carpocapsa pomonella* (L.))	(23)	Granulosis	(17)
Corn earworm (*Heliothis zea* (Boddie))	(9)	Nuclear polyhedrosis	(4)
Cotton leafworm (*Alabama argillacea* (Hübner))	(22)	do	(4)
Fall armyworm (*Laphygma frugiperda* (J. E. Smith))	(19)	do	(4)
Red-banded leaf roller (*Argyrotaenia velutinana* (Walker))	(10)	Granulosis	(11)
European spruce budworm (*Choristoneura fumiferana* (Clemens))	(6)	Nuclear polyhedrosis	--
Salt-marsh caterpillar (*Estigmene acrea* (Drury))	(18)	do	(12)
Yellow-striped armyworm (*Prodenia ornithogalli* Guenee)	(21)	do	(14)
Tobacco budworm (*Heliothis virescens* (F.))	(9)	do	(15)
Alfalfa looper (*Autographa californica* (Speyer))	(20)	do	(7)
Pink bollworm (*Pectinophora gossypiella* (Saunders))	(1)	Cytoplasmic polyhedrosis	(22)

[1] Authority for rearing method.
[2] Authority for isolation of virus.

(1) Beckman, Bruckart, and Reiser 1953, (2) Bergold 1949, (3) Bergold 1953, (4) Chapman and Glaser 1915, (5) Glaser 1928, (6) Grisdale 1963, (7) Hyslop 1912, (8) Ignoffo 1964a, (9) Ignoffo 1964b, (10) Redfern 1963, (11) Schoene and Sibold 1952, (12) Steinhaus 1949a, (13) Steinhaus 1949b, (14) Steinhaus 1949c, (15) Steinhaus 1957, (16) Smith and Rivers 1957, (17) Tanada 1964.

The following are personal communications: (18) Dunn, P. H., (19) Hamm, J. J., (20) Henneberry, T. J., (21) Hill, O. A., (22) Ignoffo, C. M., (23) Redfern, R. E.

[*Heliothis virescens* (F.)], and that of the cabbage looper [*Trichoplusia ni* (Hübner)]. Bioferm Corporation and Nutrilite Products, Inc., are experimenting with virus production, using modifications of Ignoffo's methods. We are hopeful that such efforts will increase and diversify as time goes by.

This progress brings up the obvious question--What must we know about such a viral preparation before it is finally available to the public as a commercial product?

In the United States, there are two agencies directly responsible for regulations regarding the use of pesticides; namely, the Food and Drug Administration, Health, Education, and Welfare, and the Pesticides Regulation Division, U.S. Department of Agriculture. The Food and Drug Administration is responsible for establishing the levels of tolerance permitted for pesticides and their use on consumers' goods; whereas the Pesticides Regulation Division is responsible for approving proof of efficacy, registration, and labeling of each product. Whenever proof of safety of a candidate pesticide is given, an exemption of tolerance can be granted by the Food and Drug Administration. I think the requirements of these agencies necessary for labeling a product and obtaining level of tolerance or exemption of tolerance are scientifically exemplary and will serve here as an indication of the proper treatment of a potential virus-control agent.

First, a method of production of the product with substantial techniques for standardization and uniformity must be demonstrated.

Second, means of assurance that undesirable or extraneous biotypes are eliminated must be devised, especially when a living organism is involved.

Third, the efficacy of the viral product must be demonstrated by the results of thorough field testing against the specific insect host on all its host plants.

Fourth, the safety of the product for vertebrates and for beneficial insects must be established by applying a protocol of tests that has the approval of the regulatory agencies.

I think it is quite obvious that the fulfillment of the first three requirements can be started by Government agencies, but that commercial interest and investigation are necessary before production and efficacy in the field can be established.

With regard to the last requirement (i.e., safety for other life forms), insect pathologists had concluded that insect viruses were innocuous for warm-blooded animals. Until recently no formal extensive tests had been carried out.

A survey of serologists working with insect viruses was made, and it was concluded that 28 species of viruses from 26 species of insects have been injected into 6 species of vertebrates, during the serological investigations over the past few years. The astounding fact that emerged was that, with one exception, not one animal has died exhibiting suspicious symptoms; all animals referred to either were sacrificed after several months or are still alive today. The one exception was a guinea pig in Dr. Krywienczyk's laboratory that died of unknown causes, 8 months and nine bleedings after injection of the virus. (Aizawa, Steinhaus, Stoddart, Rivers, Bergold and Krywienczyk, Smith, personal communications.)

Since such findings can hardly be considered proof, no matter how interesting, a protocol of tests was proposed by the Entomology Research Division to the regulatory agencies in the U.S. Government and was approved. These tests included intravenous, intracerebral injections of polyhedral virus and freed virus particles in mice, per os feeding of virus to mice, intraperitoneal and intradermal, allergenicity injections in guinea pigs, and inhalation tests in both species. The protocol of tests will soon be published as part of a report on the testing of the H. zea and T. ni nuclear polyhedrosis viruses. It is adequate to state here that the findings regarding these viruses support the past attitude that these micro-organisms are harmless for vertebrates.

The main point is that we now have a clear-cut procedure that can be followed to carry any of the worthwhile micro-organisms from the scientist's workbench to the final commercial product with adequate safeguards for public safety accounted for.

Lest I make the whole process sound too easy, allow me to point out that many problems still exist; for example, problems of storage, bioassay, formulation, and competitive diseases in rearings still remain partially unanswered. However, this move to actually produce the microbial control agents is a giant step toward accepted use of microbes in control programs.

How will these micro-organisms be used? In our relative ignorance at this time, but with a thought for the possibility of resistance to these specific diseases, we generally lean toward the integrated control technique, which involves the use of small amounts of insecticides along with the micro-organisms. This type of treatment would protect the host plant from other species of pests, kill the target insect by infection with the specific disease, and hopefully keep the target insect off balance so that the chance of buildup of a resistant insect would be more remote.

In conclusion, I have only one prediction to make: I am confident that insect pathology is destined to have a major role in insect control in the future. If enthusiasm and cooperation continue among interested workers throughout the world, as in the past 20 years, that day will come very soon.

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THE ROLE OF BIOLOGICAL AGENTS IN THE CONTROL OF WEEDS

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Plant abundance is primarily determined by the climatic, edaphic, and biotic factors of the ecosystem. For many years man has been a part of this ecosystem; however, it is only recently that he has developed an appreciation of the dynamic equilibrium existing among the elements of his environment and of the role he is able to have in shifting the balance. By understanding why a weed occurs where it does and the factors that have led to its present abundance, man can sometimes effect subtle changes that permit temporary or permanent economic benefits.

Of the three prime factors determining plant distribution and abundance, the easiest to manipulate is often the biotic. Included among the biotic influences are the effects of the plant itself on the environment; the indirect effects of shade, soil composition, and structure; the direct effects of parasitism, pollination, and symbiosis; and the effects of competition among plant species. The relative importance of these factors in regulating plant numbers and distribution has been poorly understood; this misunderstanding has created doubt as to the usefulness of each within the biological control program. However, on the basis of recent successes through the introduction of new plant parasitic organisms, scientists have begun to take a greater interest in the role of biotic agents and to reevaluate their use. Huffaker (1959) and also Wilson (1964) summed up the role and importance of the different agents. I will attempt to summarize the role of certain biotic factors in weed control, including a few notes on recent developments and ideas.

In considering the use of biotic agents, we should keep in mind that weed control is basically a problem in applied ecology and that the biotic elements of the plant community constitute a set of tools whose usage warrants consideration along with other methods of control. Beirne (1963) pointed out the advantages and disadvantages of biological control for insects, but they are equally valid for weeds. At its best, the method produces "... permanent, self-perpetuating, self-increasing control without human intervention other than to initiate this process." However, it is "... slower in reducing the pest population, often less effective and commonly less certain than chemical pesticides."

Man, in his exploitation of natural resources, has created a variety of situations that offer special opportunities for development of weeds. Planting widespread areas with crops not adapted to exploit the full resources of the habitat and poor land management are but two examples of such unwise exploitation (Harper, 1960). Because of the variety of situations that man has created, the biological approach to control of weeds is not always applicable and will depend on the stability and complexity of the plant community, the degree of weed control desired, the botanical position of the weed, the biotic agents available with which to work, and the imagination and ingenuity of the research worker.

The arsenal of available biotic agents ranges from those organisms with a facultative dependence on the weed plant to the strict, obligate phytophagous parasite. The nonspecific herbivores often exhibit varying degrees of polyphagy and as such can be utilized only in limited situations. Their attack on the pest plant does not depend on its stage of development, although certain periods of growth may be preferred, but is merely coincidental with their general search for food.

Examples of weed control by facultative agents include the use of chickens and geese to control nutgrass (Cyperus rotundus L.) in cultivated areas (Mayton et al., 1945), or geese alone for weed control in cotton (Miller, 1961). The manatee from the rivers of British Guiana have been used for water weed control (Bertram and Bertram, 1962). Israeli carp are being tested in California against water weeds (Berry, 1960), also the aquatic snail (Marisa cornuarietis (L.)) (Seaman and Porterfield, 1964).

To be effective, the feeding must occur within a restricted or fenced area enclosing the weedy species and the control agent, with the concentration of the agent controlled by man. The method involves management problems similar to those encountered in handling grazing animals. The snail or similar type of agent will often clean an area of all extraneous vegetation, regardless of the botanical position of the plants, and thus finds use where clean cultivation is desired. As noted, this method could be used in crop areas, aquatic situations, or even in limited range areas where the weed has not spread to any great extent. Control by this means is often not self-perpetuating, and because of its denuding effect does not add to the stability of the community. It is also important that the weeds thus grazed upon are not toxic to the biotic agent.

The obligatory phytophagous parasite, as opposed to the facultative agent, is limited in development to a particular plant or narrow group of plants, and its life cycle is closely tied to the developmental cycle of the host. This close tie to the host hampers its use in cultivated areas, especially where the catastrophic effects of harvesting and cultivation periodically interrupt the plant-parasite cycle. Most obligate parasites used for weed control have been insects, with their greatest use and success involving perennial host plants in undisturbed areas. Some examples of these successes include the work on cactus (Opuntia inermis DC.) and other Opuntia spp. with the moth Cactoblastis cactorum (Berg), the cochineal scale Dactylopius spp., plus other insects. Klamath weed (Hypericum perforatum L.) had infested approximately 2,333,000 acres in California, but was later reduced to 1 percent of this area after the introduction of beetles of Chrysolina spp. (Huffaker, 1959).

Although the perennial plant introduced into a noncultivated area offers what appears to be the ideal situation for the obligate phytophagous parasite, this kind of parasite is now finding use in controlling annuals and biennial weeds, both native and alien species, plus aquatic and parasitic plants. One advantage of the specific agent is that it searches out the weed pest, and thus its value is enhanced in both widespread and inaccessible areas.

According to Beirne (1963), there are three ways of applying biological control: "... by preserving, and facilitating the increase of, existing natural enemies; by adding new kinds of natural enemies, and by adding natural enemies, existing kinds or new, in quantities." Each of these methods--conservation, introduction, and redistribution of control agents--will be discussed with regard to weed control.

BIOLOGICAL CONTROL BY CONSERVATION

The practice of biological control by conservation requires a knowledge of the biotic elements present in the plant community. It also requires a thorough knowledge of their biologies and their overall ecological relationship to the community, with particular emphasis on their role in relation to the weed problem. Ideally this knowledge should include a familiarity with all the biotic factors mentioned previously.

In the past, we often considered that when a weed is a problem, the biotic agents present, whatever they may be, are obviously not exercising control and we should search for new species to introduce. However accurate this statement may be, if we are to attempt biological control, we should note and evaluate the role of the biotic factors already present.

The parasitic fauna associated with introduced weeds is often limited, depending on the methods and the time the weeds were introduced and how closely related the exotic species may be to native plants. Insects feeding on closely related native plants may, in all likelihood, attack the new species. These insects tend toward polyphagy (Frick, 1964); however, their lack of specificity seldom warrants this development for control purposes.

For native weeds, the associated fauna may be extensive and already capable of exerting control under favorable conditions. One example of such a weed is the native sagebrush (Artemisia tridentata Nutt.) and its insect parasite, Aroga websteri Clarke. This insect is capable of denuding its host plant, and in some years destroys thousands of acres of sagebrush, sometimes permitting return of the native grasses, which, in turn, enhance the range feeding value. With some native plants, however, certain faunal elements have developed a dependency on the weedy species, which dependency leads to a conflict of interests when destruction of the plant is promoted. Because sagebrush is a major plant in the diet of antelope and deer, the Fish and Wildlife Service personnel decry any efforts to spread or conserve A. websteri (Ritcher and Dickason, 1964).

Another instance of insect action on a native plant is the attack on shadscale, (Atriplex confertifolia (Torr. & Frem.) S. Wats.) by the scale insect Orthezia annae Cockerell on the roots and a moth, Eumysia idahoensis Mackie, in the crown. Their combined action may lead to the death of this plant in central Idaho, with subsequent invasion of the area by Halogeton glomeratus C. A. Mey., a weed pest (Mackie, 1957).

Biological control by conservation is one aspect of weed control that has received little attention. Contingent upon evaluation of those agents already present in the problem area, preservation and increase of these agents may develop into a useful weed-control tool.

BIOLOGICAL CONTROL BY INTRODUCTION

Biological control through introduction of new agents has been the most popular and successful of the methods utilized to date. In one sense, it is the easiest to apply of the three methods and can be attempted with a minimum of understanding of the plant pest or agent to be introduced. However, to be utilized fully, thorough knowledge of the plant and its parasites is required.

Introduction of phytophagous parasites is contingent on their proved specificity and safety. These elements involve an understanding of the parasite host-finding-and-host-selection behavior, plus the requirements for development, reproduction, and maintenance of the species. Most of this work has been with insects.

Studies indicate that phytophagous insects perceive and accept the plant host with the help of certain plant chemicals, and that these chemicals confer specificity, often according to taxonomic plant groupings (Harris, 1963, 1964; Andres, 1965). When these chemicals are present throughout a relatively wide range of plants, the phytophagous parasites found on one species can sometimes be used against a weedy species within the same group, but outside the current distribution of the parasite. Thus, the search for biotic agents may be extended to areas other than where the pest weed grows and may be especially useful in the search for parasites attacking native weeds.

Within the group of plants circumscribed by chemical stimuli that aid the insect in finding and feeding upon the host, we often discover a smaller number of plant species to which the insect is limited for one reason or another. Sometimes these limitations appear to be nutritional. Adult weevils of Microlarinus spp., currently being used to combat puncturevine (Tribulus terrestris L.), are polyphagous in the absence of their normal host, but develop oöcytes and oviposit only in the presence of Tribulus spp. or closely related genera of the Zygophyllaceae (Andres and Angalet, 1963). Adult weevils of Phrydiuchus spp., under consideration for control of Salvia aethiopis L., will feed to varying degrees on several labiates, but can develop eggs only on certain species of Salvia plus the related Lycopus europaeus L. and Melissa officinalis L.

Within the host range delimited by feeding and nutritional requirements, the species susceptible to attack may be further proscribed by factors of plant-growth habit, form, and texture. Weevils of Phrydiuchus spp. did not oviposit on plants otherwise chemically and nutritionally adequate to support them if the plants lacked a basal rosette. In addition, larvae of Phrydiuchus spp., the progeny from weevils forced to oviposit on certain plants, failed to penetrate the stem or exited after brief attempts at feeding (Andres, 1965).

Those insects that do not feed directly on the host plant prior to oviposition are also guided to specific plants by chemical as well as physical stimuli, which also govern the selection and ovipositional behavior.

These are only a few of the factors that govern host specificity, but they are the ones currently relied upon to guarantee the safety of introduction. Evaluation of the feeding response of free living larvae and adults has been emphasized in this regard and has followed two approaches. In island areas with limited agricultural crops, such as those in Hawaii, starvation tests are carried out with several economically important plants regardless of their taxonomic relationship to the pest weed. If little or no feeding occurs, release of the parasite is generally approved. Exclusion tests of this type have been used in most of the control programs already described.

For release in areas of more diversified agriculture, we attempt to delimit the plants, eliciting the feeding response by exposing the phytophagous parasite to species of varying taxonomic relationship to the weed pest. We assume that if plants closely related to the weeds do not contain the proper phagostimulant, the more distant species would be even less likely to elicit feeding and thus are safe from attack. We often include a minimum of related and nonrelated economic plants to eliminate special concern. We can also attempt to identify chemically the feeding stimulant present in the host plant and to correlate its presence or absence with the actual feeding results. This second approach contributes more to the fundamental knowledge of insect feeding habits than the limited exclusion tests.

Synchronizing the developmental cycle of the host to the mechanisms of insect diapause, aestivation, oöcyte development, and to the temperature threshold of insect activity contributes to host specificity, permitting the insect to conserve its reproductive energies to specific plants and plant parts. The seed fly *Hylemya seneciella* (Meade) on tansy ragwort enters a pupal diapause after it exits from the flower head in July or August. Its emergence as an adult the following spring is timed to the appearance of flowers on *Senecio jacobaea* L. The temperature threshold of activity of the Scotch broom seed weevil (*Apion fuscirostre* (F.)) controls the time that the adult emerges from hibernation to when the buds of *Cytisus scoparius* (L.) Link develop. Oöcyte formation in this insect takes place only in the presence of developing buds and flowers, and the insect will oviposit only on the broom pod. The adult weevils of *Phrydiuchus* spp. on *Salvia* spp. emerge and feed at the time of spring plant growth, aestivate during the summer dormancy, and feed and oviposit in the fall with the resumption of *Salvia* growth.

Although host specificity assures that the control agent will not attack economic plants, it does not guarantee successful control. Past parsite introductions and their success led to attempts to correlate the type of insect with the degree of control obtained. Dodd (1960) considered the insect and the part of the host attacked, noting that the leaf-feeding and plant-sucking species, most of which had more than one generation per year, were well to the fore. The diversity of the agents and their modes of attack led Wilson (1964) to conclude that the insect parasites giving control will eventually include phytophagous species of all types and that their ability to control a plant will not be readily evident.

It is unlikely that we will ever be able to predict with all accuracy the success of an introduction, although failure would imply that we lacked an understanding of the critical factors involved, which, in turn, would reduce the possibility that we could manipulate the environment to suit our purposes. It should be kept in mind that a parasite's objective is not to kill the host but to obtain energy to survive through the host with the maximum amount of parasite survival.

The growing weed passes through a series of physiological and chemical changes, periods of active food production and storage, periods of dormancy, flowering, etc. Throughout the growth cycle the plant is also subjected to periods of stress, at which time the environmental factors limiting its distribution and abundance approach, or exceed, its inherent tolerances. Much research on the tolerance of plants to feeding damage was conducted during range management studies, but may be considered applicable here.

The following generalizations from the text on "Range Management" by Stoddart and Smith (1955) illustrate briefly some of this work. In the spring a plant utilizes 75 percent of its winter root reserves to produce 10 percent of its spring growth. Also "...food storage reserves are at a minimum during periods of greatest growth, reaching a maximum in late autumn." "Where food supplies are low, forage plants are most subject to damage by grazing and undesirable plants are most easily killed at this time by mowing or spraying." In addition to the periods of physiological stress "...it must be kept in mind that grazing injury may be associated more with soil moisture and opportunities for regrowth than with physiological stage of development."

Thus, one of the first steps in selecting an agent for biological control is an understanding of the weed's developmental cycle in relation to weather and growth rate. Selection of a biotic control agent is a matter of energy relationships and knowing which species will remove the most energy from the plant at the critical periods of development. The removal of plant biomass is impressive, but if done at the wrong time, it will not affect plant survival. Synchronization to the host plant becomes of prime importance, with climatic adaptation of the agent to the weed environment being one of the first considerations.

The beetles of *Chrysolina* sp., used to control *Hypericum perforatum* L., were synchronized to feed on the spring and fall growth of their host in the United States. Removal of new growth just prior to summer and winter dormancy prevented manufacture and storage of food reserves, which resulted in reduced root development and eventual death of the plant. That these beetles failed to control the weed in

Canada was a direct result of climatic asynchronization (Harris, 1962).

Although we can attribute the major successes in biological weed control to the action one or two insects as the control agent(s), asynchronization of a phytoparasite and its host may require the introduction of additional agents before effective control is achieved. In Hawaii, the introduced tingid Teleonemia scrupulosa Stal attacks the foliage of Lantana camara var. aculeata (L.) Moldenke during the warmer months, but allows the plant to recover during the remainder of the year. Subsequent introduction of the leaf-feeding Lepidoptera Hypena strigata F., Syngamia haemorrhoidalis (Guenée), and Catabena esula (Druce), which attack the plant during the cooler months, complements the work of T. scrupulosa by denuding the plant the remainder of the season and causing plant death (Davis and Krauss, 1962). Control has been excellent where rainfall is less than 40 inches per year, but poor in wetter areas. Additional insects have been released to increase control in the wetter areas (Davis, personal correspondence).

It is more likely that multiple species releases will give effective control over wider areas unless there is evidence that a competitive intolerance between parasites might result.

Increased understanding of phytoparasite host specificity and synchronization has led to using insects to control weeds in a variety of habitats. Absence of a vegetative stage at some time during the cycle of annual weeds, plus their often erratic germination, gave rise to the concern that phytoparasites used for their control might shift their attack to economic hosts. Synchronization of the specific parasite to a host guarantees the safety of introduction, since it demonstrates its dependence on the plant.

Adult weevils of Microlarinus spp. are polyphagous in the absence of Tribulus terrestris and can live one entire summer without feeding on this host, but they develop eggs and oviposit only in the presence of Tribulus spp. Their dispersal at the time of host absence guarantees against significant feeding damage to other plants, although high concentrations of weevils may cause temporary scarring on other plant species. The success of weevils of Microlarinus spp. in Hawaii has been attributed to the tendency of its regular annual host to act as a weak perennial, plus the presence of the endemic perennial Tribulus cistoides L. The continual reproduction and feeding of the weevils on both plants have resulted in such large populations that the plants are dying outright. (Davis, personal correspondence).

The moth Heterographis fulvobasella Ragonot overwinters on Halogeton glomeratus as a pupa or prepupa and emerges at the time of plant germination (Drea and O'Connell, 1964). The cerambycid beetles Mecas saturnina J. LeConte and Nupserha antennata Gahan diapause as larvae in the soil during the absence of their annual host Xanthium spp. and complete their development under favorable spring temperatures and moisture conditions (Stride and Straatman, 1963).

Release of the flea beetle of Agasicles sp. on Alternanthera philoxeroides L. (Mart.) Griseb. is one of the first attempts at aquatic weed control with an insect. Insects were released on the National Wildlife Refuge at Savannah, Ga. The life cycle of this beetle is synchronized to the plant's development by temperature, and the insect becomes active at the time of plant growth in the spring.

Plant diseases are also among the phytoparasites of potential use in plant control. Wilson (1964) noted that the fungus Alternaria cuscutacidae sprayed onto Cuscuta cupulata Engelm., which attacks Lucerne in Russia, gave protection for three croppings. Huffaker (1959) cited other examples of the effects of disease.

BIOLOGICAL CONTROL BY PERIODIC RELEASE OR REDISTRIBUTION OF BIOTIC AGENTS

Introduction in the weed area of phytophagous agents has been confined primarily to inoculative releases, after which the parasites were left undisturbed to act on their own if established. The cyclic nature of many biological systems suggests that better use could be made of native and introduced biotic agents. Through periodic colonizations these agents could be reestablished in borderline areas where they have died out owing to irregular, severe climatic conditions. Through periodic releases they could also bring established colonies to greater working strength at critical stages in the weed cycle. Wilson (1964) cited progress made with the cochineal scale Dactylopius sp., which is systematically distributed each year to control the cactus Opuntia aurantiaca Lindl. Through periodic releases we can maintain a continual pressure on the weedy plant and overcome any asynchronization between the phytoparasite and the host. Release of large numbers of phytoparasites for immediate eradication of a weed has not been attempted. The practicality of such a technique is doubtful. It would depend on value of the land occupied by the weed, degree of control desired, and agents to be used.

Success of a periodic release program depends on a suitable supply of the biotic agent. If field populations are not readily available, artificial propagation is necessary, which limits the technique primarily to multivoltine species adapted to artificial culture conditions. From the standpoint of economy, both host and phytoparasite cycles should be reduced to a minimum. Plant diseases may also be amenable to artificial propagation technique.

Another possibility to overcome asynchronization of plant and parasite would be to artificially culture small plots of the weedy species to foster phytoparasite development, with subsequent spread to the natural weed population.

An effective adjunct to biological control of weeds is a well-planned land-management followup program. The niche vacated by the weed will be filled by other plants, the species of which can be controlled somewhat by man. By planned grazing and other techniques, plus a reseeding program, we can bring pressure against the weed, often enhance the effectiveness of the phytoparasite, and help stabilize regrowth of the entire plant community.

Biological control of weeds is still a new field, the full potentials of which we have not yet realized or tested. As already noted, when a weed problem arises, biological control should be considered simultaneously with other control methods and not as a last resort. As a result of previous successes, the interest developed in the method has led to further study of the technique.

Nonspecific agents are most effective in controlling weeds when they are confined to limited areas. Specific agents, however, can be used over wider areas; their use is limited only by their degree of host specificity, their lack of damage to plants of economic importance, and their climatic adaptations.

Weed control through importation of insects has succeeded mainly with plant families containing few members of economic importance. The closer the relationship of a weed to an economic plant, the fewer the host-specific agents available and the narrower the margin of safety. Since there is a "...tendency towards weediness to run in certain families, e.g., Compositae, Cruciferae, Gramineae..." (Harper, 1960) and since these families also contain several economic plants, we must devise new systems to evaluate the safety of introduction rather than to reply primarily on exclusion or starvation testing methods. Preoccupation with safety has caused us to focus attention on the feeding aspects of phytophagous parasite behavior. We have overlooked the fact that the host plant represents not only a source of food but the habitat of the insect, which, in turn, provides items other than nutrition. These factors should also be evaluated as to their role in determining host specificity.

When we begin to understand how to conserve the biotic agents already present, as well as the effects of soil fauna on seed reservoir, we will be able to use them more effectively for biological control of weeds. In addition, utilization of periodic release and colonization techniques will increase the effectiveness of a given biotic agent in a control program. Thus, making use of the full potential of biotic agents in weed control will depend mainly on our ability to understand the forces of the ecosystem and our ingenuity to manipulate them in the desired direction.

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BIOLOGICAL METHODS FOR THE CONTROL OF PLANT DISEASES AND NEMATODES

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Economically profitable methods of at least partial control by use of chemicals and resistant varieties have been developed for a great many plant diseases and parasitic nematodes. Despite this fact, crop disease losses in the United States average about $4 billion per year, or nearly one-tenth of the potential annual production (41). Several crop diseases of aerial plant parts and a large number of soilborne diseases and nematodes have by no means been brought under significant control. Many of the uncontrolled pathogens have such a wide range of host plants that no feasible crop rotations can be devised; or they are so unspecific and omnivorous in their nutritional requirements that finding resistant varieties appears to be a remote and time-consuming possibility. A few diseases of aboveground plant parts and several soilborne diseases and nematodes may also be difficult, unprofitable, or inadvisable to control with pesticides.

The difficulties may arise from lack of effective pesticides, need of relatively large amounts of expensive pesticides, and inactivation, decomposition, or accumulation of pesticides in soils or in other habitats. They may also arise from problems of diffusion and contact between the pesticide and the parasite (53). Therefore, since encouraging and profitable results may not always be in prospect in the chemical treatment of these diseases and nematodes, biological or "natural" control may be the best possible approach.

DEFINITION OF BIOLOGICAL CONTROL

Biological control, which is as ancient as recorded agricultural history, includes direct or indirect use of biological factors by changing the microbiological equilibrium in or around the infection court so as to eliminate or suppress the pathogen or nematode. Successful biological control implies encouragement of the beneficial organisms that share the same niche with the parasite and creation or augmentation of deleterious effects on the development, multiplication, survival, and virulence of the parasite. Biological control may be broadly defined to include control effected indirectly by roots of higher plants, as for example the use of decoy crops to induce germination of resting spores or sclerotia of fungi and the cysts of nematodes (31). Biological control may also be broadly defined to include control effected indirectly by changing the metabolism of the plant, through exogenous supply of specific nonfungicidal substances that may bring about changes in host physiology and increase resistance to attack.

In this paper we are not concerned with introducing biological control as a modern method of pest control. We are concerned with understanding the complexity of the problem that stems from numerous microecological, microbiological, physiological, and biochemical processes in the plant environment. We are concerned with interactions of micro-organisms mediating survival of plant parasites and with the basic principles that underlie interactions of specific pathogens and associated antagonistic micro-organisms. We are concerned with collecting, analyzing, and interpreting fundamental information of this sort in order to devise practices needed for a widespread utilization of biological control.

METHODS OF BIOLOGICAL CONTROL

Direct Introduction of Antagonistic Micro-organisms to Soil or Plant Tissues

Many workers have attempted to control plant parasitic bacteria, fungi, and nematodes by use of the activities of antagonistic micro-organisms and predators (5, 16, 26, 30, 31, 39, 91). One of the approaches employed is the direct inoculation of infested soil or plant tissues with cultures of antagonists or predators (26, 30).

Direct Introduction of Antagonists or Predators to Soil.--Several investigators thought that direct introduction of antagonistic or predacious micro-organisms into soils, in the form of dried spores, appeared the most feasible method for large-scale application and utilization of such micro-organisms for biological control. Direct introduction of antagonists to soil to control biologically such economically important and widespread fungal pathogens as Fusarium, Helminthosporium, Pythium, Rhizoctonia, Sclerotium, Verticillium, and others, exerted a slight and temporary biological control (16, 30).

Several unsuccessful attempts have been made to introduce nematode-trapping fungi into soil to control plant parasitic nematodes (27, 28, 50). Efforts by Mankau (51), however, to isolate the nematode-trapping fungi introduced into field soils were also unsuccessful, although the fungi rapidly and readily colonized sterile soils. In these studies, and in those with introduced antagonists to control fungal and bacterial pathogens, significant biological control has been achieved only when sterile soil or synthetic media were inoculated with the parasite and the antagonist or predator. The addition of antagonists or predators to nonsterile infested soils either had no effect on the parasites or the effect was slight and transitory.

Direct Introduction of Antagonists to Plant Tissues.--The introduction of antagonists, with or without nutrients to control pathogens of aerial plant organs, has not met with any great success (16). Newhook (59) introduced spores of *Cladosporium herbarum* and *Pencillium* sp. to control *Botrytis cinerea*, which attacks tomato fruit after becoming established on dead petals. Biological control of *B. cinerea* was completely successful when the antagonists were introduced into recently dried petals, but only 30 percent successful when introduced to petals that had dried for several days. Under natural conditions, however, inoculation was not necessary, because the antagonists had been isolated from dry petals to begin with.

Mention of experiments to control bacterial plant diseases biologically by introducing phages in the appropriate vicinity of the pathogen is worthwhile despite the fact that this subject was covered in a recent review (16). Most interesting experiments were performed by Keil and Wilson (38) on the control of peach bacterial spot with *Xanthomonas pruni* bacteriophage. In greenhouse experiments, these investigators obtained significant control of the disease either by mixing the phage with a suspension of *X. pruni* inoculum and then spraying it on the plants or by applying the phage as a spray and allowing it to dry on the plants before inoculation. Control with phage was equal or superior to that obtained with zinc sulfate plus hydrated lime.

On the other hand, attempts to control plant diseases biologically, by inoculating plant seeds with antibiotic-producing saprophytes, have met with considerable success. Wright (94) in England obtained *Pythium* control of white mustard seedlings by dusting seeds with spores of antibiotic fungi. Of three strains of *Trichoderma viride* (a soil-inhabiting fungus) tested against the *Pythium* disease, a gliotoxin-producing strain was more effective than a viridin-producing strain; and that strain was more effective than an antibiotically inactive strain. In experiments by Gregory et al. (33), alfalfa seedlings were protected from damping-off incited by *Pythium debaryanum* by the incorporation of *T. viride* spores into a pellet mixture surrounding the seed. Tveit and Wood (89) reported very good control of *Fusarium* blight of barley seedlings by inoculation of the seed or soil with *Chaetomium*, some species of which produce antibiotics in culture.

Biological control methods, involving purposeful introduction of antagonists or predators to soils or plant tissues, are subject to certain general features and limitations. Some workers believe, or at least hope, that once an organism is found to be antagonistic against a specific pathogen, it can be added to soil or to plant tissue to control a plant parasite. That alone seems too much to hope for, because the antagonist usually comes from soil or plant tissues to begin with. As Pramer (74) recently pointed out, antagonists and predators are normal inhabitants of soil, and their simple addition to soil usually has only a transient effect. If micro-organisms are to be used for biological control of plant diseases and nematodes, it is not their presence but their growth and predaceous activity that must be encouraged. The practical importance of micro-organisms as biological control agents would appear, then, to be dependent, to an extent far greater than observed with the use of beneficial insects, on the favorable extrinsic factors and on microenvironmental conditions expected to upset the status of existing micro-equilibrium.

Specific or Nonspecific Modification of Microenvironment

Effective antagonists and predators and conditions suitable for them are more likely found in environments in which a serious infestation has been alleviated through micro-environmental changes favorable to the action of antagonists naturally present. Conditions that favor the antagonists will have to be sought in these microenvironments and not on synthetic media. This opens the way to the control of plant diseases and nematodes by specific or nonspecific modification of the environment that is shared by the parasite and the antagonist or predator.

Amendments.--The possible use of organic and inorganic amendments to enhance, selectively, a particular segment of the micro-flora to such an extent that a suppression of a parasite may be brought about has been extensively studied. The pioneering work of Millard and Taylor (54) on utilization of amendments to control potato scab was followed by great attempts to control plant diseases and nematodes by amendments. The literature has been exhaustively reviewed in recent articles (16, 30, 31, 39, 77, 78, 85, 91). Since this type of preferential disturbance of established microbial equilibria by use of amendments is of extraordinary significance in soilborne plant pathogens and nematodes, a few examples will be cited only from this particular group of plant parasites.

Linford and coinvestigators (43, 45) obtained control of the root-knot nematode of pineapple by heavy applications of organic matter. Chopped-up pineapple plants were used as the organic supplement and cowpeas as the test plant for estimating populations of *Heterodera marioni* in soil after treatment. Linford et al. (45) suggested that "decomposition results in a greatly increased population of total nematodes in the soil, and that these, in turn, support the building-up of large populations of plant and animal forms destructive to nematodes, including nema-capturing fungi, nontrapping, fungal parasites, predacious nematodes, and predacious mites." Johnson (35) found that several mature dry crop residues, when added to nematode-infested soil, appreciably reduced root knot of tomatoes. The effectiveness of the amendments depended on the incubation temperature (36). Some attempts to control nematode populations by adding organic matter, with or without supplemental nematode-trapping fungi, were unsuccessful (26, 50). Details of the work of Linford and coworkers and of other similar research were summarized recently (5, 26, 74).

Elegant in their inception and execution were the experiments by Garrett (29, 30) on the use of amendments to control *Ophiobolus graminis*, the "take-all" disease of wheat. *O. graminis* spreads in soil along roots of its host plant, but it can also exist in a resting stage in dead host tissue (29). The rate of growth of the pathogen along roots decreases with the increase of carbon dioxide in the surrounding atmosphere. Microbial activity, stimulated by the addition of organic matter and by cultivation aimed at close packing of soil around roots, undoubtedly results in an increase of CO_2 in the immediate vicinity of the pathogen. This kind of indirect control of of actively growing mycelium along roots is distinct from the biological control of resting mycelium of this pathogen. Garrett (30) showed that addition to infested soil of organic matter, poor or lacking nitrogen, resulted in considerable loss of viability of the colonizing resting mycelium. The effectiveness of organic matter depended on its nitrogen content. He (30) suggested that supply of organic matter relatively poor in nitrogen resulted in great increase of the numbers of saprophytes, which assimilated the mqcelium as a source of nitrogen.

Soil organic amendments may be expected to be ineffectual for biological control of a large and important group of soil-inhabiting fungi, such as *Rhizoctonia*, which has marked ability to colonize competitively organic matter lying in or on the ground. Considerable conflicting evidence exists concerning the effectiveness of various amendments and supplemental nitrogen for the suppression of *R. solani*, an omnivorous and economically important pathogen. A given amendment was found to be effective in one location at one time and ineffective in a different location or at a different time. Also, supplemental soil nitrogen either increased or decreased the *Rhizoctonia* disease of several crops, depending on conditions, time, crops used, amendment used, and the like.

At Beltsville, Md., we found that some organic amendments suppressed *Rhizoctonia* in soil and others were ineffective, yet some increased the competitive saprophytic activity of the pathogen and the amount of disease incited (17, 18, 65). Saprophytic behavior and therefore survival of *Rhizoctonia* was affected considerably by the carbon-to-nitrogen balance of the colonizable substrates (20, 66). In fact, in experiments where carbon/nitrogen ratios of substrates had been modified by the addition of glucose or ammonium nitrate, to produce a range of carbon/nitrogen ratios, the carbon-to-nitrogen balance determined the extent of competitive colonization and survival of *R. solani* (66). A decrease of substrate carbon/nitrogen ratio, by the addition of increasing concentrations of nitrogen, produced a marked increase in competitive saprophytic activity of the pathogen and an increase in the longevity of active fungus mycelium in colonized tissues. Loss of viability, on the other hand, was hastened by supplementing the substrate with energy material that raised the carbon/nitrogen ratios.

That the saprophytic behavior and survival of *Rhizoctonia* may be affected by the carbon-to-nitrogen balance of amendments was shown in more detail in our experiments in which cellulose powder, oat straw, or soybean hay, and a nitrogen source were combined to produce a wide range of carbon/nitrogen ratios of the amendments before their incorporation in *Rhizoctonia*-infested soil (20). Saprophytic activity and survival of *Rhizoctonia* were slightly suppressed by cellulose and greatly enhanced by nitrogen. By the cellulose-nitrogen combinations activity was most significantly suppressed within the carbon/nitrogen ratio of 40 to 80 one week after incorporation, 40 to 100 after 3 weeks, and 40 to 200 after 5 weeks. By the oat straw-nitrogen combination saprophytic activity was significantly suppressed almost within the same carbon/nitrogen ratio. By the soybean hay-nitrogen combination, however, saprophytic activity was suppressed at a carbon/nitrogen ratio range lower than that of cellulose and oat straw.

The foregoing results on *Rhizoctonia* help us to understand why so many conflicting reports have been published on the efficacy of amendments for biological control of plant diseases. It is now realized that the value of organic matter for purposes of biological control may be directly related at least to its carbon/nitrogen ratio which, among others, determines the extent of availability for decomposition. The carbon/nitrogen ratio may be more important than the absolute amount of carbon and nitrogen added to soil in affecting behavior of root-infecting fungi and nematodes. Effect of the carbon-to-nitrogen balance on the rate and degree of amendment effectiveness, to suppress saprophytic activity, may be the result of a "flare-up" of particular groups of microorganisms stimulated within a range of carbon/nitrogen ratios predetermined by inherent microbial characteristics and microenvironmental factors.

Manipulation of Environment Through Cultural Practices

Cultural practices such as crop sequence or crop rotation and crop management constitute the best known, the most widely adopted, and perhaps the oldest method of biological control of plant diseases. In practice today one group of pathogens is kept under a fair degree of control by use of crop rotation and soil management practices that retard the build-up of the pathogen. This method of biological control is applied with some pathogens that have narrow host ranges and relatively short persistences in the absence of their specific hosts. One of the most successful cases of biological control of a soilborne disease by crop rotation is that of the "take-all" disease of wheat in Great Britain (32).

Rotations with nonhost of poor host crops have long been used for reducing harmful nematode populations (15). In general, rotations have been most effective when a single species of a relatively host-specific nematode is involved in crop losses. Rotations are not considered to be effective when several species are present, because one of them may be increased by a rotation that decreases another. The most complete investigations of the effects of rotations on nematode populations come from studies of control of *Heterodera* spp. Jones (37) showed that populations of *H. schachtii* decline at the rate of 40 to 50 percent each year in the absence of host plants. Depending on the initial population level, up to 8 years may be required for the reduction of populations of this nematode to acceptable levels.

Biological control through crop sequence has long been ascribed to antagonistic effects of natural soil microfloras associated with crop residues and root excretions, accumulation or depletion of toxic ions, increasing host resistance, decoying activities of root excretions and organic supplements, effects of nutrients, and prevention of contiguity in time and space of susceptible plants and virulent pathogens (15, 84). Crop sequence control measures have on occasion been dramatically effective, but they are often very erratic and reveal great voids in our knowledge of scientific principles and in the advancement of the arts of crop management.

Indirect Biological Control Mediated by Plant Excretions

In 1924, Noble (60) showed that spore germination of *Urocystis tritici*, the cause of flag smut of wheat, is stimulated by a variety of substances and by roots of several nonhost plants. For over a quarter of a century this important discovery has become only a textbook curiosity. If nonsusceptible decoy crops could be found as a stimulus to propagule germination of plant parasites, an indirect partial or complete eradication of the parasite could be obtained before the advent of a susceptible crop. During the last 25 years, many workers have attempted to control soilborne plant pathogens and nematodes by using the root exudates of nonsusceptible plants to promote resistant propagule germination in the absence of susceptible hosts.

This kind of biological stimulation for spore germination (8), or egg or cyst hatching (44) by host-plant diffusates, is well known. White (90) reduced infection of potato tubers by *Spongospora subterranea*, the potato wart fungus, in field experiments by planting in a heavily infested soil a nonsusceptible decoy crop of Jimson weed (*Datura stramonium*). Macfarlane (49) reduced infections of test cabbage seedlings by *Plasmodiophora brassicae*, the club root organism, by growing short-term catch crops of ryegrass or crucifers in infested soil before planting the susceptible host. Recently Schroth and Hendrix (80) found that chlamydospores of *Fusarium solani f. phaseoli*, the dry root-rot organism of beans, germinated in close proximity to seeds and roots of many nonsusceptible plants. After germination, the number of propagules increased in the rhizospheres of tomato, lettuce, and corn, but decreased in the rhizosphere of onions. Onion could therefore be used as a possible decoy crop to reduce survival of this important pathogen in soil.

Selective Control Through Physiological Changes

Very few cases of selective biological control through changes in host metabolism have been reported (23). Research in our laboratory on the nutrition of *Aphanomyces*, the cause of a serious root rot of peas, radish, and sugarbeets, indicated that the oxidation state of sulfur had a profound effect on the growth and sexual reproduction of the pathogen (19, 64). Sulfur-containing amino acids, especially methionine, were most favorable for growth and sexual reproduction of the pathogen. Subsequent studies (68, 69) on the effect of various sulfur sources on the development of *Aphanomyces* root rot of peas led to the discovery that methionine was able to prevent disease development completely, even though it was in no way detrimental to the fungus.

Further studies were made (70) of the effect of methyl-containing amino compounds and related substances with and without sulfur in their molecules on the expression of disease symptoms. These studies showed (1) that the oxidation state of sulfur of the compounds and root rot severity were not related; (2) that all compounds partially or completely effective against the expression of disease symptoms possessed methyl and amino groups in their molecules; (3) that the position of the methyl group in the molecule was very critical with respect to control; and (4) that the effect of these methyl-containing amino compounds was not on the disease-causing organism, but rather on the expression of disease symptoms.

These studies suggested a host response to the methyl group in conjunction with the amino group. They also suggested that transmethylation in plants may be an important process related to disease resistance. The concept of transmethylation was further supported by the demonstration (21) that pea plants were able to convert homocysteine, a precursor of methionine lacking a methyl group, to methionine, which possesses a methyl group and which, in turn, suppressed the disease.

Transmethylation reactions occur not only in animals but also in several plants. The methyl group from methionine and other compounds was transferred intact to form the methoxyl groups of lignins in barley and tobacco plants (10) and the methyl esters of pectinic acid in radish plants (79). The middle lamella of pea roots contains pectinates with an unknown degree of esterification, whose breakdown by the fungus enzymes leads to maceration and root-rot development. Recent studies (1) on pectolytic enzymes of *Aphanomyces* showed that the parasite produced pectic acid depolymerase, but not pectin methylesterase. Depolymerase, constitutively produced, rapidly degraded pectin and reduced the viscosity of pectates without significant release of reducing sugars. Pectin and pectinic acids of increasing methyl esterification were more resistant to attack by the fungal enzyme than demethylated pectins or pectins of low methyl content.

MECHANISMS OF BIOLOGICAL CONTROL--ANTAGONISM

Finally, lest it appear that plant pathologists and microbiologists exaggerate the applied aspects of biological control, this review may reasonably include some basic considerations in regard to the mechanisms of biological control. Specific mechanisms of biological control of plant diseases and nematodes are highly elusive because of the complex nature of the problem and limitations in approaches and methodology. Antagonism has been perhaps the most widely recognized mechanism. In a recent symposium in Berkeley, we (63) proposed to place antibiosis, competition, and mycoparasitism and predation under the general term of antagonism and to accept the term in its broadest meaning, i.e., as encompassing all possible microbial associations and interactions, in which at least one of the interacting microbes is harmed. This breaking down of antagonism was also suggested by Park (73).

It is appropriate to say at this point, however--lest it appear that antagonism has been correctly implicated in all instances as the mechanism of biological control--that in many cases conclusive evidence is still lacking as to whether there is any relation between the relative abundance of organisms that antagonize a given pathogen or nematode and the ability of that species to survive in its microenvironment. This difficulty usually stems from the fact that antagonism on agar plates may be absent when the situation is studied under natural environmental conditions (42) and vice versa; organisms that show no antagonism in cultures may be antagonistic in a natural environment (88). The second point was shown by Slykhuis (83), who found that, of a number of antagonists to Fusarium culmorum, the most active forms did not produce antibiotics in culture.

Antibiosis

Antibiosis, a form of antagonism, was recognized as being mediated by specific or nonspecific toxic metabolites of microbial origin, by lytic agents, and by fungitoxins (34, 63, 78). It is still mainly conjectural as to whether antibiosis is important in biological control of plant pathogens and nematodes. The significant line of evidence is based on the fact that microenvironmental conditions necessary for biological control and the requirements essential for expression of various phases of antibiosis are parallel.

In our work with Rhizoctonia we (17, 65) showed first that incorporation of crops residues produced a marked increase in the abundance and activities of nonpathogenic micro-organisms and a concomitant decrease in the Rhizoctonia disease of beans. Green amendments when added to Rhizoctonia-infested soil, substantially increased total numbers of soil and rhizosphere fungi and streptomycetes, as well as the total number of soil bacteria; and they also suppressed the Rhizoctonia disease (65). Decomposing green corn and oats stimulated the highest number of streptomycetes antagonistic to R. solani, gave the susceptible host the best and longest protection, and decreased the competitive saprophytic activity and survival of the pathogen in soil. Sudangrass, green snap beans, buckwheat, and no amendment (control) resulted in fewer antagonistic streptomycetes than corn and oats, in the highest disease, and in the highest saprophytic activity and survival of the pathogen.

Antibiosis in the control of soilborne plant pathogens, mediated by rising populations of antagonists, does not preclude other mechanisms of biological control during amendment decomposition. This was suggested by Garrett's experiments (30) on O. graminis and our own (67) on carbon dioxide and its effects on Rhizoctonia. In naturally or artificially infested soils, we observed considerable inhibition of the saprophytic activity of Rhizoctonia in soils permeated by atmospheres containing various CO_2 concentrations. The inhibitory action of CO_2 on the saprophytic phase of Rhizoctonia was shown by a stright-line dosage-response curve obtained from the values for percentages of inhibition of colonization by increasing CO_2 concentrations. The parasitic phase of *Rhizoctonia* was more sensitive to CO_2 than its active saprophytic phase; and the latter was more sensitive to CO_2 than its saprophytic surviving ability within precolonized substrate segments (62, 71).

Antibiotics.--Although there is as yet far too little available information, the accumulated evidence suggests that specific harmful microbial metabolites or antibiotics may be involved in antibiosis. Two questions concerning antibiotic substances in soil have repeatedly been asked and extensively debated: *Are antibiotics produced by micro-organisms in their natural microhabitats? If so, do they really mediate ecological relationships that result in the suppression of plant parasites*? The existing evidence now suggests that in an least some cases the well-known antibiosis between saprophytes and plant pathogens is actually associated with the production of antibiotics by the saprophytes (6). In specific soil, or in such plant-surface microhabitats as segments of decomposing organic debris, plant residues, seedcoats, and soil-root interfaces, a local concentration of antibiotic substances may be maintained at a rate sufficiently high to exert a profound effect on biological control, even though the overall concentration is too low to be detected by conventional extraction procedures. For instance, the adpressed growth habit of *T. viride* around hyphae of *R. solani* would insure not only direct parasitism but also a local concentration of gliotoxin and viridin toxic to the pathogen. A concentration sufficiently high to be toxic to *R. solani* would not be attained if the two organisms were growing far enough apart.

Whether antibiotics are produced in natural habitats is perhaps only of academic interest. If however, antibiotics are produced in natural amended habitats, or in natural organic microhabitats, this would be of extraordinary practical significance, because production after amendment is a result of upsetting dynamic soil equilibria by a treatment that can be applied by any farmer. Wright (92, 93) showed that energy-yielding materials in soils are critical in the production of antibiotics, and that local concentrations of antibiotics may be produced in the vicinity of suitable carbon sources. Since soil micro-organisms tend, by necessity or ecological preference, to be concentrated in such sites, the antibiotics formed may attain sufficiently high concentrations to exert significant ecological effects.

Lysis.--Antibiosis as a mechanism of antagonism mediated by specific antibiotic substances may not be the sole mechanism responsible for biological control. Other mechanisms, such as lysis of fungal mycelium, are also important. Considerable evidence is now available that lysis, a form of antibiosis, is an important mechanism of biological control. Lysis may be enhanced by saprophytes, associated with decomposing amendments and other agricultural practices. Recent work by Sequeira (81) on lysis of *Fusarium oxysporum* f. *cubense* in the presence of sucrose and other amendments, and work by Mitchell and Alexander (55, 57) on chitin, substantially support the contention that lysis affected by amendments is an important mechanism of biological control. Not only mycelia of plant pathogenic fungi may be subject to lysis or disintegration and destruction (46, 47) but also resting fungal propagules (72, 86).

Lysis of fungi has been reported (11, 12) and certain plant diseases have been controlled experimentally with mycolytic micro-organisms (9, 13, 22, 40). For instance, Mitchell and Alexander (55, 56, 57) found a correlation between the amount of disintegration of mycelium or other fungal parts and reduction of *Fusarium* diseases. Chinn and Ledingham (13) reported lysis of *Helminthosporium sativum* germ tubes after spores were stimulated to germinate by soybean meal, molasses, and vitamin C. A similar biological control mechanism of *Phymatotrichum* root rot of cotton was reported by Mitchell et al. (58).

Despite all the recent progress on lysis, very little is known of the exact mechanism and the precise role taken by antagonistic microbes. Lysis may be mediated by exposure of fungal mycelium to enzymes produced either by the micro-organisms that participate in the decomposition of special amendments (55, 57) or by an increase in staling as a result of saprophytic growth of associated organisms (73); or it may be brought about by nutrient deficiencies, internal metabolic processes, and toxins (7). Some investigators have shown that lysis may be due to the combined effects of antibiotics and some unidentified soil factors (82) or to the combined effect of antibiotics and enzymes produced by lytic organisms (46, 47).

In a recent paper (61), the carbon-to-nitrogen balance of amendments appeared to be of great importance in determining the amount of lysis. Considerable mycelial lysis of three root-infecting fungi was observed by oat straw of carbon/nitrogen ratios 30, 50, and 85. The amount of lysis increased with increase of carbon/nitrogen ratio of amendments; and this increase was more pronounced with *R. solani* and *Verticillium albo-atrum* than with *F. solani* f. *phaseoli*. The least destruction of mycelia was caused by unamended soil, by soil supplemented with nitrogen only, and by oat straw of carbon/nitrogen ratio 10.

Fungistasis.--Specific toxic metabolites and lytic agents may not be the only mechanisms responsible for antibiosis and biological control. Antibiosis may also assume the form of fungistasis, a form of natural toxicity to fungi in soils manifested by nonspecific inhibition of spore germination. In 1953, Dobbs and Hinson (24) demonstrated that germination of inactive fungal propagules in soil and in plant rhizosphere is not generally limited by lack of nutrients but by the almost universal presence, in natural soils, of inhibitory and fungistatic factors. Spore germination of fungi is stimulated by counteracting the inhibitory effect of soil fungistasis by plant excretions and various organic amendments (48). Fungistasis was found in a variety of natural soils (24, 48), but is not exhibited in autoclaved soils. Fungistasis may be due to diffusible toxic metabolites in natural soils (48). Some investigators (48) were able to reinstate fungistasis by infesting autoclaved soils with common soil saprophytes now known to produce antibiotics in culture.

Despite extensive studies on fungistasis believed to be of biological origin, there still remains the question of the specific origin and nature of the widespread soil fungistat. Nevertheless, plant pathologists and microbiologists have not failed to understand the extraordinary microecological significance of this process. Let us visualize some fungal propagules lying in soil matrix or in plant rhizosphere. Addition of organic amendments will overcome fungistasis and start the time clock for a series of unpredictable and predictable events. These will involve germination of propagules of soil saprophytes, soil antagonists, competitors, predators, and root-infecting fungi. Some propagules will germinate and germ tubes will lyse (13). Others will germinate normally and grow through soil matrix, organic debris, or roots. Others will, to say the least, grow and produce toxic metabolites. Still others will germinate and precociously sporulate (3). The overcoming of fungistasis then will result in immense, unpredictable, and explosive disturbances of the soil microbiological equilibrium. These disturbances may result in direct or indirect alterations of inoculum potential of a given pathogen. It is up to the research man to discover the course of events that would lead to the reduction of the disease potential of a specific plant pathogen.

Competition

In addition to antibiosis, competition is another important mechanism of antagonism. Competition is considered here in its strict sense as an associative effect in which one organism adversely affects another in the struggle for some limiting factor of the environment. If competition, which may be exerted whether or not a competing organism produces an antibiotic, takes a role in biological control, this must apply almost exclusively to soilborne diseases and nematodes. Marshall and Alexander (52) suggested that "competition for nutrients is a significant means of ecological control among members of soil microflora and, together with competitive interactions for space and oxygen, may be the major factors governing the biological control of soil-borne fungi."

Several cases of competition for energy-yielding materials are known (14). Garrett (30) ascribed the depressing effect of decomposing ryegrass meal in soil on *O. graminis* to the fact that numbers of micro-organisms are so greatly increased inside and around the added amendments that they consume all available nutrients, especially nitrogen, and thus create starvation conditions for the *Ophiobolus* mycelium. Skinner (82), with the ingenious use of bentonite, was able to distinguish in sterile sand cultures between the inhibition of *F. culmorum* by *Streptomyces albido flavus* caused by antibiosis and that caused by competition for nutrients. Rapid growth of the competitive organism because of the presence of abundant glucose probably lead to the exhaustion of one or more other nutrients.

Competition for nutrients, when further studied, may prove an important mechanism of biological control of soilborne plant pathogens and nematodes. The intricate and diverse microecological conditions mediating the balance among micro-organisms that are in competition with each other for energy-yielding materials will undoubtedly be of considerable practical and theoretical singificance.

Hyperparasitism and Predation

Plant pathogenic fungi and parasitic nematodes may be directly parasitized by other hyperparasites. Hyperparasitism may be important in the survival of fungi possessing dormant propagules, because it will slowly eliminate these propagules by attrition. A good example of this type of parasitism is that of sclerotia of Sclerotinia trifoliorum by Coniothyrium minitans (87). In inoculation experiments the hyperparasite killed more than 80 percent of the sclerotia of S. trifoliorum within 11 weeks. Drechsler (25) described hyperparasitism of oöspores of Pythium. Boosalis (2) found that R. solani, in unsterilized soil amended with green organic matter and kept at 28° C, was parasitized by Penicillium vermiculatum and Trichoderma sp. Even under the most favorable conditions, however, only 18 percent of the Rhizoctonia hyphae were parasitized. Several other examples of hyperparasitism were summarized recently (4, 5, 16).

Several fungi and bacteria are known to be parasitic on fungal pathogens attacking aerial plant parts. Darluca filum, for example, a hyperparasite, ramifies throughout pycnidia and aecial sori and urediospores and teliospores of cereal rust fungi. This hyperparasite, however, as well as other hyperparasites of rusts, was unable to reduce rust epiphytotics in the field (16). Ciccinobolus cesati, a hyperparasite that can be cultivated in artificial media and added to plants, parasitizes hyphae and conidiophores of Erysiphe graminis (the cereal powdery mildew fungus). Ciccinobolus, however, has seldom reduced powdery mildew epiphytotics in nature because of its inability to establish itself and build up large numbers (16).

About 50 known species of predaceous fungi capture and kill nematodes in soil (26). There is great hope that nematode-trapping fungi may some day be successfully used for biological control of nematodes. This hope stems from the fact that, despite their remarkable morphological adaptation, nematode-trapping fungi are not obligate predators. Most of them exist in soils as saprophytes, and some are known to grow on agar media. Recently Pramer and his associates (75, 76) found that the trap formation in nematode-trapping fungi is induced by a metabolic product of nematodes, a product named "nemin" extracted from worm-free culture filtrates. It is, however, too early to evaluate the significance of this finding in the biological control of nematodes.

Although hyperparasitism has been observed in some habitats, the evidence for its significance in biological control is circumstantial (4). As Boosalis (4) and Boosalis and Mankau (5) have pointed out in recent review papers, we are today faced with great difficulty to assess the importance of hyperparasitism and predation accurately. It is even more difficult to evaluate the significance of hyperparasitism and predation on the biological control of plant pathogens and nematodes. Our inability to determine the actual role taken by hyperparasitism and predation for biological control stems from the fact that most of the work on this subject has been performed in vitro, and also from the fact that plant pathogens and nematodes live in a rather obscure environment difficult to observe.

CONCLUSIONS

It is clear that some of the important problems and questions touched upon in this paper confront the plant pathologist and microbiologist with attractive and challenging problems, the elucidation of which will have great practical and theoretical significance. Only with extraordinary progress in microbiological and biochemical research methods, accompanied by thorough, integrated, and exhaustive research on fungal and nematode behavior, will our knowledge be widened. Only then will biological control measures cease to be merely empirical, unreliable, and inextensible and become sound and practical.

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APPLICATION OF STERILIZATION TECHNIQUES FOR CONTROLLING AND ERADICATING INSECT PESTS

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Few animal species can tolerate a drastic reduction in their reproductive potential that at best may be only high enough to outweigh the natural hazards present in their environment. When sterility can be induced in animals without destroying mating competitiveness and these sterile individuals can then be introduced into the natural environments in overwhelming numbers during a sustained period, the natural population subjected to such treatment will in due time vanish.

About 1937, E. F. Knipling, of the U.S. Department of Agriculture, developed a unique new method for population suppression that was based on this concept. Since 1937, the method has passed beyond the hypothesis stage and demonstrated its effectiveness against populations of the screw-worm fly (Cochliomyia hominivorax (Coquerel)), the melon fly (Dacus cucurbitae (Coquillett)), the oriental fruit fly (Dacus dorsalis (Hendel)), the Mediterranean fruit fly (Ceratitis capitata (Wiedemann)), and the Mexican fruit fly (Anastrepha ludens (Loew)). This new approach to insect control--the sterile insect release method--must rank as one of the most remarkable biological achievements of our time.

The principles involved in the sterile male release method have been documented in numerous publications, the most recent and comprehensive of which is by Dr. Knipling.[1] In the present discussion I will emphasize recent progress in practical applications of the technique for controlling populations of certain insects.

As early as 1937, it occurred to Dr. Knipling that it might be economically feasible to rear and release sterilized screw-worm flies in sufficient numbers to exceed the natural population. A colleague, A. W. Lindquist, then located at Uvalde, Tex., had observed that the numbers of screw-worm flies were exceedingly small in that area during the winter. Several methods for using released flies to destroy their own kind were then considered. The most promising approach seemed to be the release of flies sterilized with X- or gamma rays. During the next 12 years, the reactions of biologists to this self-destruction approach to screw-worm control were generally pessimistic. Notwithstanding, the possibilities, as based on theoretical calculations, continued to be too great to ignore. Consequently, in 1950, with encouragement from H. J. Muller--an eminent geneticist formerly with the University of Texas, but later with Indiana University--research to explore the sterility concept of insect population control was begun on the screw-worm fly. This research was conducted under the leadership of R. C. Bushland of the Entomology Research Division. The first studies dealt with the effects of X- and gamma rays on the reproductive behavior and potential of the insect.

When news of the screw-worm sterilization research in Texas reached Hawaii, where I was then studying tropical fruit flies, I was greatly impressed with the possibilities of utilizing sterile insects to control wild insects. Already we had advanced far in our knowledge of how to mass-rear fruit flies and could produce large quantities of these flies at low cost. Even though the early concept of the sterile male release method suggested that it would apply only to species that mate but once, theoretically at least, it seemed possible that grossly overflooding the wild polygamous tropical fruit flies with sterile insects might have a chance of effectively eliminating the flies. Insect species often undergo stress conditions that require the product of their full reproductive potential. Our thought was that an added burden of induced sterility would make it difficult for the fruit flies to survive critical periods. On this basis we began our fruit fly sterilization studies in Hawaii more than a dozen years ago. Studies of other scientists, demonstrating that radiation induced dominant lethals in competitive mobile sperm without necessarily destroying their ability to fertilize the ova, furnished an explanation of why our first results were even more promising than we had expected.

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REQUIREMENTS OF THE METHOD

Requirements that determine the feasibility of application of the sterile male release method to insect populations, as developed by Dr. Knipling,[1] are as follows:

(1) Availability of a method of inducing sterility without serious adverse effects on mating behavior and competitiveness.

(2) Method of rearing the insect.

(3) Quantitative information on natural population density at the low level in the population cycle.

(4) A practical way of reducing natural populations to levels manageable with sterile insects.

(5) Information on rate of population increase as a guide for determining the necessary rate of overflooding with sterile insects.

(6) Cost of current methods of control plus losses caused by the insect must be higher than the cost of reducing the natural population plus the cost for rearing and releasing the required number of sterile insects.

(7) If complete population control cannot be maintained because of reinfestations by migrating insects, or new introductions, the cost of maintaining complete control by continuing sterile insect releases must be favorable in relation to the costs for current methods of control, plus additional losses caused by the insect.

(8) There would be justification for employing the sterile insect release method, even if it were more costly than current ways to control or eradicate insect populations, if it provides advantages in overcoming hazards to man and his environment.

(9) Sterile insects to be released must not cause undue losses to crops or livestock or create hazards for man that outweigh the benefits of achieving or maintaining population control.

With undiminished repeated applications of sterile males, the ratio of sterile to normal insects becomes increasingly greater. Theoretically with effective overflooding, eradication of a species should be accomplished in four generations, according to the calculations of Dr. Knipling.

Some qualification of the requirement that the sterile male release method cannot be used if the released sterile insects are harmful to crops, animals, or man may be in order. Federal and State plant pest control officials are often confronted with the need to eliminate an incipient infestation of a newly introduced pest species that sometimes involves comparatively few insects. Such infestations could be overflooded effectively with numbers of sterile insects so small that the injury they would inflict could not cause appreciable harm or would be tolerated in the public interest.

Insects that reproduce by asexual means, such as aphids, do not lend themselves to control by sterile insect release methods. As indicated in the above requirements, the sheer abundance of certain pests may prevent successful use of sterile males unless such insects can be brought within reach of the technique by the use of population thinning agents, such as insecticides, cultural control, strong attractants, biological control, or other means. A basic limitation on the use of the method is inability to rear the pest insect whether artificially or on natural diets. The need to develop efficient methods for mass-rearing species for which all other requirements are met cannot be overemphasized.

THE INSECT PROBLEM

In 1952, approximately 10,000 species of insects in our country were important enough to be called public enemies in the Yearbook of Agriculture. About four-fifths of these are injurious to plant crops, since they reduce yield, lower quality, contaminate market products, or increase marketing and processing costs. The most recent estimates of losses caused by insect pests that attack these crops add up to more than $3 billion each year. Control of insect pests with insecticides has contributed much to our national growth and agricultural economy, but there has been growing concern over problems associated with insecticide usage, mostly those caused by objectionable residues. The sterility method is one of the most promising of new approaches that someday may permit us to reduce significantly the quantities of insecticide now required to control insects. An adequate, healthy food supply for our people requires good insect control.

PRACTICAL USES FOR STERILE INSECTS

Thus far, the effectiveness of the sterile male release method has been demonstrated against five species of insects. All are strong-flying Diptera. The most notable success was achieved with releases of sterile screw-worm flies. This insect infests wounds of cattle and other animals, often causing their death. However, equally significant in demonstrating the feasibility of the concept were successful western Pacific island tests involving the oriental fruit fly and melon fly. These are important tropical fruit fly species that infest a variety of fruits and vegetables and can cause great economic losses. Releases of the Mediterranean fruit fly, another major pest of tropical fruits, reduced natural infestations in partially isolated pilot tests in Hawaii and Costa Rica.

A unique, practical use of sterile flies was the substitution, in 1964, of releases of sterile Mexican fruit flies for costly and objectionable spray programs to protect against the annual invasion of this fly into the Tijuana and adjacent southern California areas.

Research on methods of sterilizing insects by radiation is in progress, with field tests under way or planned, for the following insects: Gypsy moth (Porthetria dispar (Linnaeus)), codling moth (Carpocapsa pomonella (Linnaeus)), pink bollworm (Pectinophora gossypiella (Saunders)), tsetse fly (Glossina morsitans Westwood), boll weevil (Anthonomus grandis Boheman), cockchafer (Melolontha vulgaris F.), and vinegar fly (Drosophila melanogaster (Meigen)). Our prospects appear reasonably good for the practical application of the technique against these species, especially when the method is integrated with other methods of control.

Insects that have been or are now the subjects of considerable sterilization research include the following: Corn earworm (Heliothis zea (Boddie)), tobacco budworm (Heliothis virescens (Fabricius)), tobacco hornworm (Protoparce sexta (Johannson)), sugarcane borer (Diatraea saccharalis (Fabricius)), European corn borer (Ostrinia nubilalis (Hübner)), Oriental fruit moth (Grapholitha molesta (Busck)), olive fruit fly (Dacus oleae (Gmelin)), Mediterranean flour moth (Anagasta Kuehniella (Zeller)), certain mosquitoes that may create disease or comfort threats in isolated areas, and Queensland fruit fly (Dacus tryoni (Froggatt)).

It is unlikely that the sterile insect release technique will be feasible or practical for all, or even most, of these species. However, successful application of the method against even a few of the major species could contribute materially to the overall objective of developing ways to control insects with no adverse side effects. As yet, researchers are not investigating the potential value of the method against many other insect species, present in different parts of the world, that would be favorable candidates for its application. A breakdown in behavior caused by radiation dosages required for sterilization appears to be one of the most common limiting factors. We hope that means of avoiding radiation damage, such as substitution of chemosterilants for radiation, fractionation of radiation dosage, or even selective application of radiation to only a part of the insect body, may ultimately provide solutions to the behavior breakdown problem.

Research on the screw-worm fly, conducted under R. C. Bushland at the U.S. Department of Agriculture laboratory at Kerrville, Tex., established that a dosage of 5,000 roentgens of ionizing radiation from an X- or gamma ray source, applied to 7-day-old screw-worm pupae, would impart sterility to both sexes of emerging adults. Dosages up to 20,000 roentgens did not appear to seriously affect the vigor of the flies. When normal females were mated with sterile males, the normal females laid only infertile eggs throughout their lifespan. Thus, whenever a sterile male mated with a normal female, the effect was equivalent to destruction of the female.

After the soundness of the concept of overflooding normal screw-worm flies with sterile flies to suppress reproduction had been established in laboratory studies, pilot field tests were conducted by A. H. Baumhover, O. H. Graham, and others in the Entomology Research Division, U.S. Department of Agriculture. The first sterile male screw-worms were released in a 15-square-mile area at Sanabel, Fla., at a calculated overflooding rate of 4 sterile flies to 1 wild fly, or 100 sterile flies per square mile per week. The insect population was reduced to a low point in 3 months. However, eradication was not accomplished, unquestionably because of lack of complete isolation by the narrow 2-mile stretch of water between Sanabel and the mainland.

The next pilot experiment, conducted in Curacao in the Netherlands Antilles, was eminently successful. This island has an area of 170 square miles, with 40 miles of open sea isolating it from the nearest land. Releases of 400 screw-worm flies per square mile per week eliminated all infestation in goats and other livestock within 9 weeks. The Curacao demonstration will long remain a classic in scientific achievement. It was the first time man had ever destroyed entirely an insect pest population by introducing into its natural environment sterile insects of the same species in numbers sufficient to negate the reproductive potential of the natural population.

In 1958, after the spectacular results obtained on Curacao, the Animal Disease Eradication Division in the U.S. Department of Agriculture, in cooperation with the Florida Livestock Board, initiated a large-scale program of sterile screw-worm fly releases in Florida. The purpose, of course, was to eradicate the screw-worm. The success of this program is well known. I need only add that the estimated savings to cattle growers during the past 7 years in Florida and other Southeastern States, have amounted to $140 million. Cost of the program was about $7 million, if cost of quarantine operations along the Mississippi River to prevent reinfestation is excluded. This was a remarkably profitable insect-control operation.

The Florida results quickly aroused the interest of Texan and other southwestern cattle growers. In 1962, a new screw-worm fly-rearing plant was constructed at Mission, Tex., in cooperation with the U.S. Department of Agriculture. The new fly-rearing plant, to which C. H. Husman, working with the Entomology Research and Animal Disease Eradication Divisions, contributed so much, is an entomological marvel of our times. It covers, 76,000 square feet and employs 300 people. It was built entirely with funds provided by the livestock growers and sportsmen in the Southwest. In satisfying a production quota of 100 million sterile screw-worm flies per week, the fly-rearing plant feeds and provides for 14,300,000 larvae every 24 hours. The plant has the capacity to produce 150 million flies if the need arises.

After inception of the program in 1962, the occurrence of scattered light infestations of screw-worm flies throughout the fly release area in the Southwest caused major changes in release strategy. Scattered infestations during the spring and fall periods suggested that some flies had migrated for distances of several hundred miles. Tests with marked flies demonstrated that screw-worms could travel at least 180 miles from the source of release. These findings supported the conclusion that the scattered infestations resulted from movement of normal flies into Texas from Mexico through the barrier in Mexico consisting of a zone 100 miles wide in which the sterile flies were released. Widening this zone to 200 miles and concentrating releases along watercourses where cattle and flies congregate have contributed substantially to the subsequent marked improvement in results.

During 1962, the year the program in Texas was started, 50,779 cases of screw-worm infestation were confirmed. In 1963, there were only 6,339 cases. Continued releases in 1964 reduced the number in 12 months to only 239. The protection level was estimated to be about 75 percent in 1962. Thus, the degree of control during 1964 exceeded 99.5 percent. Livestock owners in the Southwest have estimated that the savings resulting from this program, which has cost about $12 million so far, have been close to $275 million. We must agree that in terms of dollars saved, this is a highly successful, nonchemical means of insect control.

The principal obstacle to application of the sterile male release technique against tropical fruit flies is the high population density that these flies may attain in some environments. Large numbers of sterile flies must sometimes be produced to adequately overflood the wild flies. The hypothetical reduction in fertility is seldom, if ever, achieved in laboratory cages when untreated flies are overflooded with irradiated, sterile flies. We believe such a failure is caused by the loss of mating competitiveness in the treated flies owing to radiation damage and possibly to behavioral changes in the entire group of laboratory-reared insects. This loss must be compensated for by releases of larger numbers of flies. Before they attain the ability to mate, many released sterile fruit flies die during the week or more they must spend seeking proteins having the vitamins necessary for sexual maturity. This loss, which may be as high as 40 percent, must also be compensated for with increased releases. Fortunately the need for large numbers of flies can easily be met. Several species of tropical fruit flies can be produced efficiently and economically at costs as low, or lower than $80 per million.

After releases of more than 20 million sterile Mediterranean fruit flies at a semi-isolated location in Hawaii by L. F. Steiner and associates in the Entomology Research Division, infestations in preferred hosts appeared to be strongly reduced. Releases of nearly a half billion sterile oriental fruit flies on the 30-square-mile island of Rota, located north of Guam in the Mariana Islands, at rates as high as nearly 10 million per week, failed to exercise control over the wild fly population. However, the target overflooding objective of 10 to 1, as established by cage studies, was not achieved. Therefore this experiment was not considered to be a test of the sterile release method but rather one of fly production, logistics, distribution, and sterile fly behavior. Unexpectedly large numbers of flies developing in breadfruit, previously considered to be a marginal host in Hawaii, was a complicating factor. To adequately overflood populations of the oriental fruit fly, we may have to achieve an initial ratio of sterile to fertile flies of 25-50 to 1.

The melon fly was the first tropical fruit fly to be eradicated on an isolated island, again Rota. Experiences with the oriental fruit fly on Rota had taught us much, especially that scarcity in numbers of the wild population is a precious attribute. In further eradication efforts, we should take advantage of this condition whether it occurs naturally or is induced by man. With this knowledge of the importance of low-population density in the application of the sterile insect release method, a limited amount of insecticide bait spray was applied in the vicinity of farm plots where the preferred host plants of the melon fly were growing. This removed an estimated 75-90 percent of all adult flies on the island. The Hawaii fruit fly laboratory then began to release about 10 million sterile flies per week and continued the releases for an extended period, quickly achieving strong and adequate overflooding of the wild flies by sterile flies. Infestation in preferred host plants disappeared within 4 months after releases began. The overpowering effect of a heavy blanket of sterility on a wild population again had been demonstrated.

A typhoon in 1963 left a path of devastation when it passed through Guam. Among the casualties were many favored oriental fruit fly host plants. With this help from nature, the numbers of wild oriental fruit flies were greatly reduced and releases of sterile flies in January 1964, again by L. F. Steiner and associates, quickly eliminated the remaining normal flies from all of Guam. In this experiment, owing to the low natural population, the release of a few million sterile flies each week resulted in a ratio of perhaps 100 sterile flies to 1 fertile wild fly and quickly eliminated the insect from the island.

An interesting and important use of sterile males is their distribution to provide quarantine barriers against insect invasion and spread of established infestations. Occasionally some insects are able to avoid detection at ports of entry in spite of all precautionary measures taken to protect against them. If the new insect is allowed to breed unmolested, infestations may quickly attain such proportions that profitable production of the crop infested will soon be impossible. Eradication programs to eliminate or contain incipient infestations usually have been based on the application of insecticides, the only means heretofore available. The dosage of insecticides required and the overall cost of control are essentially the same whether the natural population of an insect is high or low. But this rule does not apply when sterile insects are used.

Each year Mexican fruit flies that develop in mangoes, and perhaps in other fruits transported from interior Mexico into the Tijuana area, have threatened subtropical fruit production in southern California. Cooperative programs conducted by the U.S. Department of Agriculture and Defensa Agricola in Mexico, in which protein hydrolysate-malathion bait sprays have been utilized, have been carried on to eliminate the newly emerged flies before they could make their way into California and become established there. A 3-mile protection zone along the border in California was also sprayed by the California Department of Agriculture each year to destroy migrating flies that crossed the border. The spray programs were costly and a public nuisance, even though the number of insects present each year probably did not exceed more than a few thousand. In Tijuana, often the only access to backyard patios where host plants to be sprayed are located is through the houses of property owners. How much longer the spray program in Mexico and California might have been carried on without serious objection by the cooperating public already had become a moot question.

An easier way than applying insecticides to take care of the fruit fly problem in Tijuana and southern California began to unfold in Mexico several years ago. At the Entomology Research Division's laboratory in Mexico City, studies conducted by R. H. Rhode showed that the Mexican fruit fly could be sterilized with practical dosages of radiation, without serious behavior breakdown. Releases of sterile flies in several small-scale pilot tests at semi-isolated locations appeared to suppress populations or inhibit normal increases in infestations. The first few tests conducted by Rhode suggested strongly that the sterile release method might be completely effective if applied to entire populations, especially where a higher ratio of sterile to wild flies could be maintained.

In the meantime, J. G. Shaw, also of the Mexico City laboratory, was evaluating chemosterilants as possible means of sterilizing Mexican fruit flies. In tests with several dozen candidate materials, one known as tepa (tris(1-aziridinyl)phosphine oxide) was effective. Shaw and his associate, M. Sanchez-Riviello, then developed a highly efficient pupal dip technique for sterilizing the Mexican fruit fly. The pupae were dipped in a 5 percent solution of the chemosterilant. Apparently as the adult Mexican fruit flies emerged, they received a sterilizing dose by coming in contact with residues of tepa on the outside of their pupal cases. The dip method appeared to have an advantage over the radiation method of sterilization because the males sterilized with chemicals were more normal in mating competitiveness than males sterilized by radiation of pupae.

With the concurrence of the Dirrecion General de Sanidad Vegetal in Mexico, a test of the efficiency of chemosterilized Mexican fruit flies was arranged in a semiisolated mango grove at Bebedero in Morelos State. The results were phenomenal. Strong overflooding was quickly achieved, and no infestation was found in the mangoes until some immigrating flies began to appear after most of the crop had been harvested. An interesting thing about this test was the failure of the sterile females, introduced with the males, to damage the fruit. Their efforts to insert ovipositers were largely futile, and the mangoes for the most part were unmarked by fruit fly stings.

The next step in the use of chemosterilized Mexican fruit flies was an historical one. For the first time man employed sterile insects to protect agriculture against invasion by a foreign insect pest. Weekly releases of sterile Mexican fruit flies were initiated in Tijuana and its environs early in 1964. Complete dependence was placed on the sterile flies, and the spray programs were abandoned. Normal flies were caught in traps during the summer months of 1964, but the 4 3/4 million sterile flies that were liberated did their job well. There has been no evidence of establishment of the Mexican fruit fly either in Tijuana or California. Thus, the use of a caretaker population of sterile insects to prevent establishment of a foreign insect pest became a practical reality in 1964.

The results of this first year of sterile fly releases in the Tijuana area again confirmed our strong belief in sterilazation techniques. Substitution of a biological procedure for the use of insecticides was an especially pleasing justification for our interest in new approaches to insect control. Our belief is that sterile insects will have growing usefulness in quarantine and regulatory programs as time goes on.

STERILE INSECTS AS BARRIERS TO SPREAD OF INFESTATIONS

I briefly mentioned use of a barrier zone of sterile screw-worm males to prevent fertile females produced in Mexico from reaching Texas. The theory behind establishment of this zone is that young flies emerging in the zone or entering it would soon mate with sterile flies and thus be rendered infertile before reaching Texas. The width of the barrier needed may be critical. Obviously if a fertile screw-worm could fly all the way through such a barrier, some infestation would be expected. This situation occurred in Texas early in the screw-worm control effort. A wider barrier the following year greatly reduced the number of fertile female flies that crossed over it.

The barrier concept of using sterile insects may also serve other special purposes. Some insect pests introduced from abroad are still present in limited areas only. A band of sterile insects at the periphery of such an infestation should be effective in preventing further spread, or at least in greatly retarding the rate of increase of the infested area. The width of the band of sterile insects required for this purpose would depend on the flight habits of the insect.

In Panama there is a major new citrus development of nearly 10,000 acres. This acreage is threatened by the Mediterranean fruit fly, which has spread from Costa Rica. In eradication campaigns in Florida, a bait-spray barrier of a mile or even less, usually prevented spread of this fly to uninfested areas. A barrier zone of sterile medflies 1 to 5 miles wide might be surprisingly efficient in holding the Panama infestation in check. Undoubtedly some normal medflies would get through such a zone before attaining sexual maturity. However, many of the sterile flies would move with them. The normal flies would also be so widely distributed that it might be difficult for a fertile male and a fertile female to be present in the same area for successful mating, especially since this tropical fruit fly has no strong sex attractant, as many insects do.

Often discussions of the possibility of using the sterile male release method end on a pessimistic note, especially when the insects involved are widely distributed throughout extensive areas, or even over entire continents. It does not seem necessary to exclude consideration of an insect pest because of the size of the infested area. If all other requirements are favorable, a barrier could be used to partition the infested area, then sterile insects could be applied piecemeal to the infested terrain. We believe that certain insects may someday be eradicated in this manner from whole continents. The now numerous instances of eradication of isolated insect infestations in our country, some of these extending over large areas, and the recent successes with sterilization methods, are monuments to the attainability of eradication. Impetus should be given to research that will furnish ever new and effective eradication procedures that do not create objectionable side effects.

There is now worldwide interest in the use of sterile males to contain infestations of or eradicate entirely highly damaging insect pests. A major project to eradicate the olive fruit fly is underway in Greece. For some time entomologists have been investigating sterilization techniques for control or eradiction of certain costly forest insects and insects that attack animals, tobacco, grain, forage crops, vegetables, and fruits. Entomologists in Australia have had intensive sterilization research underway on the Queensland fruit fly. Studies thus far have yielded exciting successes, sometimes only a promise of success, and sometimes dismal failures. The failures need not discourage us. Before attaining success in our fruit fly sterilization studies we had to learn many things, sometimes at great expense, before various components began to fit together and the requirements of successful usage became apparent.

I have referred to the expense of our sterilization research. Each insect species must be considered separately, since its response to sterilization may be different than that of another insect. No matter what the cost, and even if only one key insect pest out of 10, 20, or 30 succumbs to the magic of overflooding with sterile males, the prize is worth all research effort. Think back to the screw-worm profits. Nearly $400 million in savings! Less than $20 million expended in application of the sterilization principle!

I have not yet discussed the use of sterile insects to control insect pests without complete eradiation as the goal. With many pest insects, we would only have to delay development for one or two generations to permit the crop to be harvested without serious damage. The release of sterile insects may be the ideal way to accomplish this purpose. When crops appear in the spring, the numbers of insects present are often few. Restricting development of these with comparatively small numbers of sterile insects may give control, especially when the insects do not fly long distances. This use of sterile insects deserves much research attention.

I have also failed to discuss the use of chemosterilants to sterilize populations of insects in nature. We are making much progress in our research on chemosterilants and have discovered numerous effective materials. Our hope is that we will soon find safe chemosterilants or ways of using them without hazard. The bonus effects possible from sterilizing field populations directly without having to release insects sterilized in the rearing plant are a challenge for future research.

CONCLUSIONS

Progress made in research on sterilization procedures for insect population suppression permits the following conclusions:

(1) Releases of sterile males in numbers sufficient to grossly overflood wild insect populations provide an ideal nonchemical means of combating key insect pests when the latter satisfy basic requirements of the method.

(2) Eradication or control of a number of important insect pests should be feasible through application of the sterilization principle, no matter whether the insects are present in isolated infestations or have widespread continental distribution.

(3) The sterile male release method will not be feasible for use on many insect pests because of incompatible mode of existence, behavior, method of reproduction, or the obstacle of excessive numbers unless the excessive numbers can be overcome with practical population thinning procedures.

(4) Most effective use of the sterile male release method will be to snuff out or maintain continuous control of low-density populations achieved through application of other control procedures or resulting from natural causes.

(5) Released sterile insects may serve an important role in regulatory, eradication, and control programs as barriers to the establishment of introduced foreign pests or the spread of established infestations.

(6) Although the cost of sterilization research and application of sterile insects may be high in contrast to that involved in developing broad-spectrum insecticides, there is no end to the benefits that will result when eradication has been achieved.

(7) The still largely untapped potential of sterilization methods for eradicating or controlling insect pests should be exploited fully in the years to come and receive all possible support.

VETEBRATE PEST CONTROL BY BIOLOGICAL MEANS

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"Biological control" is really an indefinable label applied to fighting biology with biology, especially in limiting the growth of or in actually reducing the size of populations. All animals and populations of animals are limited and abetted in their success by that indivisible trinity of physics, chemistry, and biology that makes up their ecological niches and body physiologies. Biology never acts alone.

Neither is the label "vertebrate pest" definable in any satisfactory way. Homo sapiens (a biological agent) emerges as the single outstanding pressure impinging for better or for worse upon the ecological niches and populations of vertebrate animals. Man is responsible either directly or indirectly for altering the conditions that permit or prevent the continued existence of vertebrate populations. Whether an animal or population of animals constitutes a "pest" is purely a biological judgment on the part of man incriminating himself for creating or imagining the biological problem. Therefore, all pest control is biology versus biology via biology. The struggle is not so much man against nature as it is a struggle of humans against human nature.

The ruby-throated hummingbird (Archilochus colubris) that cross-pollinates flowers is a pest of horticulture. A pest is only a pest at a given time, place, and situation. At any other time, place, or situation the pest may be a blessing--nor is a pestless world either attainable or desirable. I suggest, therefore, as a preamble to this discussion that the best biological means of vertebrate pest control is the adoption of a charitable and philosophical approach to those animals that we ourselves cause to be called pests. May we learn to control our own biological numbers, activities, value systems, and tolerances. Daniel B. Luten's (1963) essay, "How Dense Can People Be" is worth the reading.

In the meantime, how might we resolve crises in managing overpopulations of vertebrates by pitting biology against biology? There are two general choices of approach: (1) Manipulate the ecological niche to decimate the organisms, i.e., Biotic Control, or (2) manipulate the organism to decimate itself in its ecological niche, i.e., Biogenetic Control. This paper will consider both of these approaches as they apply to nuisance fish, mammals, and birds. Most of the examples will be drawn from birds, as most of my work has been done with that class.

From examining the various means of biological control there evolves an appreciation of a hierachy of values attached to the selection of one means over another. These values revolve around effectiveness, selectivity, subtleness, timing, humaneness, self-containment, economy, reversability, practicality, etc. Biological control can be grossly crude or finely sophisticated.

Laboratory physiologists on the one hand and armchair zoologists on the other frequently come up with materials or theories that would seem to be of extraordinary effectiveness, but in practice they default because of the trump action of some one of the just-mentioned hierarchy of values. Wildlife biologists have learned to buy with caution, for the proving ground of a biological control agent is on the actual ecological niche of the target wild population.

MANIPULATION OF ECOLOGICAL NICHE TO DECIMATE ORGANISMS, i.e., BIOTIC CONTROL

With this approach we again have two choices: (1) To capitalize on the organisms' ecological requirements or (2) to capitalize on the organisms' ecological intolerances.

Biotic requirements pertain to positive features in the environment: Food, water, protective cover, breeding sites, releaser stimuli, etc. Biotic intolerances pertain to negative features in the environment: Predators, diseases, parasites, poisons, disturbance, competition, etc.

The ecological niches of animals are not simply circles or smooth spheres. Each species has a niche that can be represented symbolically as a snowflake--complex and unique. The projections of the snowflake configuration may be said to represent the animals' requirements; the indentations of the configuration are its intolerances. Usually some projections or indentations are more conspicuous than the others and are more vulnerable. Wildlife technicians call these the limiting factors; zoologists call these the isolating characters or evolutionary specializations. Every species has them--but the analogy between snow crystals and ecological niches stops here, or rather can be extended to Gestalten. Niches are more like Gestalten of the psychologists: Formed patterns of sensations and reflexes integrated and functioning in interrelationship. The totality of your awareness at this particular instant is your Gestalt. The niche, or Gestalt, is multidimensional and dynamic. The niche is different in July from what it is in June; different when the animal is hungry from what it is when satiated. The niche is also mutable, subject to evolution, as when the insect population evolves resistence to the hydrocarbon or the blackbird habituates to the scarecrow.

Biotic Requirements

Usually the more enlightened ecological approach is to deal with the positive features in the environment, the animals' requirements--to put an embargo on vulnerable requisites in short supply.

One of the pressing conflicts between vertebrate numbers and man's economic, aesthetic, and other vital interests is the recent population explosion of herring gulls (Larus argentatus) in the Northeast. Gulls plunder crops, pollute domestic water supplies, rob feeds, collide with airplanes, compete with more desirable species, and otherwise offend our tidy lives. At the turn of the century the herring gull was rare as a breeding bird in the United States. Today they are counted by the tens of thousands and have extended their breeding range south to the Carolinas. The growth of this population coincides with the growth of open-faced metropolitan dumps, sewerage outlets, fish piers, and other sources of what we might call "gurry" along the seaboard. Whether or not the correlation is causal, no one can deny that herring gulls today derive a large percentage of their food from these festering sources of nourishment. Biotic control of this scavenger could be achieved, without doubt, simply by doing away with the gurry--but doing away with it is not simple, for this involves training that most intractable of all animals, man.

Any of the countless species that we now esteem, whose habitats have been ruined by man, could have become pests if their biotic requirements had been more fully met rather than less fully met. The overabundant elk (Cervus canadensis) of Yellowstone National Park is a case in point.

Environmental control at the site of the problem is usually the most satisfactory answer to vertebrate pest problems. Continental population reduction is seldom if ever the reasonable solution. The next best thing to removal of local food supply is the removal of the vegetative cover immediately around the problem site. Proper grazing practices tend to eliminate mice, ground squirrels, and rabbits in agricultural areas where they constitute a pest.

The most extraordinary example in my experience of lack of biotic control was seen on our inspection of the Logan International Airport in Boston, Mass., after the tragic collision of an aircraft with a flock of birds in 1960. Logan Airport was virtually a wildlife sanctuary with many small blocks of varied habitat, including ponds, lush borders, phragmites roosts, brush copses, tidal flats, and of course a garbage dump. The Boston Port Authority is doing much to change all this.

There are instances where vertebrate pests can not be controlled by removing the biotic requirements, for some species have been put into direct competition with our own, but always new, biotic requirements. Where our own requirements can not be protected by positive physical or cultural means, the population of pests must be reduced by negative means.

Biotic Intolerances

Natural predation helps keep populations in check, but there is a necessary population threshold (seldom low enough to suit our objectives), below which the predator suffers more than the prey. In very limited situations animal predators may be released with some effectiveness, as in the following two examples, but their use can hardly be generally recommended. At several Canadian and European airfields trained falcons have recently been employed to reduce the numbers of birds that present a potential hazard to aircraft operation. Raccoons (Procyon lotor) were released on islands off Massachusetts in 1964 by Dr. John A. Kadlec to discourage nesting of gulls.

Warm-water fishpond management, where the operator has the advantage of working with a closed system, is largely founded on control by predation (Swingle and Smith, 1941). Both forage and carnivorous species of fish must be stocked together in the correct proportions to assure both types reaching legal catching size. Too many forage fish result in their stunted growth. With few forage fish carnivorous fish extirpate them and then begin eating their own offspring.

The controlled harvest of surplus renewable natural resources is sound biology, good economics, and the core principle of conservation. The militancy that once rescued wildlife species from extinction is slow to relax however. It seems to be ingrained in American culture that to eat eggs of wild birds is not only illegal but also morally oblique. In 1912, my late esteemed cousin, Henry Wetherbee Henshaw, Chief of the U.S. Bureau of Biological Survey, wrote, "It is strongly recommended. . . in localities where [house] sparrows are too numerous they be trapped for table use, thus utilizing for food a bird which in many places has come to be both a public and a private nuisance," Soliocentrism, in 1965, as in 1912, is still poised to snip off noses of those who advocate blackbird pie or gull omelet.

Much too little is known about the diseases of wildlife for deliberate use of this kind of biological control at this time. There is need for a great amount of research on the subject. Similarly with the introduction of competitive vertebrate species, we can never know enough about the biology of an exotic species to predict in what direction its biological course will run once it is liberated. The deliberate introduction of the house sparrow (Passer domesticus) and the starling (Sturnus vulgaris) into North America, in part, at least for control of insects, and their competition with several native species for the essentials of life should be regarded as an outmoded concept of mongoosoid biological control.

The shortage of negative biotic tools has understandably led to the preeminence of pest control by chemical means. Dr. Walter Dykstra in this symposium has already developed this subject.

MANIPULATION OF ORGANISM TO DECIMATE ITSELF IN ITS ECOLOGICAL NICHE, i.e., BIOGENETIC CONTROL

Biogenesis, the dependence of racial survival upon individuals begetting replacement individuals, can be thwarted physiologically in wildlife species just as it can and should be in the human species. Manipulation of the rate of reproduction results in higher or lower levels of population. Theoretically the presence of a number of sterile individuals in a population should exert extraordinary reductional pressures upon that population, much greater than if the same number were killed, for those sterile individuals that are allowed to remain not only fail to contribute biogenetically to the next generation but meanwhile compete for biotic space, food, and social order.

Birth control should not be viewed as the panacea for pests however. By definition vertebrate pests are weeds--organisms with high tolerances, low requirements, and quantitative resilience. The vertebrates that we classify as pests have very steep population growth curves. Populations of many of the vertebrate pest species are probably at or near the leveled-off top of the classical sigmoid growth curve. To artificially push them off the plateau, by biogenetic control or any other means, onto the precipitous slope of the sigmoid growth curve is of no avail unless the biogenetic control effort be unrelenting or unless it be accompanied by a concurrent control of the biotic requirements that nurture the growth curve and survival rate. A half-sterilized bacterial culture doesn't remain sterile for long, neither does a reproductively inhibited population of dump-fed rats. Biogenetic control then should be viewed as an artificial means. As most pest thrive in the filth that separates us from Eden, it would be a pity to remove the pests and preserve the filth, whether it be physical or a cultural system of biologically false values.

The chain of reproduction has many links, any one of which may be broken to result in biogenetic failure. A search for link-breakers has been pursued at the Bureau's wildlife research unit at the University of Massachusetts (Wetherbee, progress reports, 1959-64). David E. Davis (1961), following the lead of Knipling (1960) in insect control, first elucidated the principle of gametocidal population control for vertebrate pests.

The following discussion will consider the recent findings in biogenetic failure via three routes of attack: Male gametes, female gametes, and embryos.

Antifecundity in the Male

Wentworth (1962) and Crawford (1962) at the Massachusetts unit reviewed the physiological inhibition of spermatogenesis and sperm sustentation in birds. Experimentally spermatogenesis has been shown to be inhibited by reduction of light, deficiency of vitamin E, altered hormonal balance, hybridization, shortwave irradiation and by the action of drugs.

The reduction of light obviously is impractical for operational use in the natural habitat.

Mammals are more sensitive to vitamin E deficiency than are birds. Carroll and Noble (1957) reported that male rats raised with a supplement of 10 percent or more by weight of erucic acid suffered a progressive reduction in spermatogenesis and became completely sterile after about 5 months despite normal growth and good health. A vitamin E antagonism is suspected. However, the use of most nutritive deficiencies in inhibiting spermatogenesis is impractical, as the diets in wild populations cannot be restricted where natural foods are available ad libitum.

The genetic isolation conferred upon the first generation of hybrid crosses is well known. Mules, be they mammalian or avian, are sterile, but who can enforce hybridization in nature, and (in contrast to work with insects) it is impractical to release large numbers of vertebrates propogated from the laboratory.

One of the management problems in fisheries is that fish tend to overpopulate or exceed the carrying capacity of the brooks and ponds. Where there are too many fish for the amount of food available, the fish grow in numbers but not in size. Anglers would rather have larger even though fewer quarry. In a closed system, such as in a fishpond, it is possible, although expensive, to kill by rotenone all the fish and restock with individuals of one sex only. This type of facultative sterility has actually been practiced effectively in the reclamation program of the Massachusetts Division of Fisheries and Game.

The hormonal balance, which regulated the formation of spermatozoa in the testis, has been a natural site of attack for reproduction prohibitionists. The administration of prolactin is antagonistic to gametogenesis and also inhibits gonadotropic hormone secretion (Bates et al., 1937). However, proteinaceous hormones cannot be administered orally and it is impractical to capture and inject enough animals from any appreciable fraction of a wild population. Androgens and estrogens and progestins, natural or synthetic, have metabolic potency when ingested by depressing the testes by way of the pituitary. Diethylstilbestrol (D.E.S)-induced capons that were once available on the poultry market bear testimony to the effectiveness of the hormonal approach to sex reversal, but those capons were produced by implantation of longlasting hormonal pellets under the skin. The ingestion of hormones (the ethinylated steroids are more effective orally than the non-ethinylated) is ineffective unless continued over an extended period, and most of these hormones are prohibitively expensive. In rats and mice an acute androgen-sensitive vulnerability to induction of permanent sterility exists within a period between birth and the 10th day of age. The vulnerability (not the sterility) disappears after the 10th day of age. Barraclough (1961) thought the physiological mode of action was through the crippling of pituitary growth.

Viviparous fishes (of no importance in fisheries management) can be sex directed by hormones, as can many species of frogs (Witschi and Crown, 1937).

Paralleling the familiar medical immunity response that develops from vaccination in the practice of disease prevention, vertebrates can be made immune to fertilization by inoculation with a vaccine containing gonadal or germinal tissues or fluids. Immunologic procedures include the formation of antigonadotrophic substances, the formation of antibodies in the agglutination process, the formation of antibodies against spermatogenesis, and even the formation of antihormone antibodies. Nelson (1961) has summarized some of this work in its application to humans. In birds, Wentworth and Mellen (1964) at the University of Massachusetts have recently induced active immunity to fertilization and suppression of spermatogenesis by means of testicular antigen. Freund et al, (1953) showed aspermatogenesis in a rodent. Until an orally effective immunity can be induced, this line of approach will have little but theoretical value to control of large wildlife population. Inoculation of elk by means of propelled syringes, however, may be a possible contemporary use of the injection technique.

The effects of ionizing radiation usually come to mind when one begins to search for a weapon of sterilization. The radiosensitivity of birds has recently been reviewed by Wetherbee et al. (ms.). It would seem that whole-body irradiation sufficient to cause irreversible sterility is too near the lethal level in vertebrates. Radionuclide ingestion might well be used against spermatogenesis, but the problems of environmental contamination are probably insuperable. High-energy microwave (radar) failed to sterilize birds or eggs under field conditions (Wetherbee, progress reports, 1959-64).

Spermatocidal drugs and chemosterilants offer the greatest potential threat to male fecundity. The numbers of compounds tested in human birth-control research are legion; those that have been tested in wildlife species and found practical are few. Jackson et al. (1961) orally administered a number of simple alkane sulfonic esters to rats and reported extraordinary results. Cumulative doses produced predictable periods of reversible sterility according to dose rate. No effects on libido were noted nor any toxic side effects. David E. Davis (1959) found that triethylenemelamine (T.E.M.) inhibited testicular recrudescence in starlings, with the testis becoming merely an interstitial organ. A limited field test on red-winged blackbirds (Agelaius phoeniceus) with this cytocide indicated a probable causal reduction in fecundity (Vandenbergh and Davis, 1962).

While T.E.M., on the basis of Davis's work, presently has the highest candidacy for operational use against male birds (in spite of negative findings that we have experienced when the compound is used on sexually active male birds), Enheptin (2-amino, 5-nitrothiazole) also has potential for special purposes. This compound tested at the Massachusetts unit has no effect on rats but has differential potencies among bird species.

Antifecundity in the Female

Although some species of vertebrates are, at least theoretically, monogamous, most are polygamous. Biological economy places more value on the ovum than on the spermatozoan in either instance, and our search for reproductive inhibitors in vertebrates has focused on the female with that good justification.

Somes (1962) and Consuegra (1962) at the Massachusetts unit have reviewed the physiological inhibition of oögenesis and ovum sustentation in birds. Mammalian antifecundity research, which of course includes the human species, has a ponderous literature and is bustling with activity. No pretense is made here of relating the findings of that science to wildlife management. However, Balser (1964) and Linhart and Enders (1964) have studied the management of mammalian predator populations (coyotes, Canis latrans, and red foxes, Vulpes fulva) with antifecundity agents. Balser's work at the Denver laboratory of the U.S. Bureau of Sport Fisheries and Wildlife is focused on upsetting the normal endocrine balance by oral administration of baits containing diethylstilbestrol (D.E.S.). His field tests indicated that 80 percent of the female coyotes taken off a treated area were reproductively inhibited (this is probably 100 percent of those that took bait) and 100 percent of those taken off a reference area showed no inhibition.

Induced sterility in game and pan fish has so far been a failure and no practical method has been devised, although with the every-day discovery of new antifecundity compounds it may be premature for aquatic biologists to be pessimistic.

We have found that the expensive progestational 19-nor steroids that currently enjoy wide usage in human birth control also have physiological potency in birds but of extremely short duration. The various androgens and estrogens bring about their classical effects, but are soon swept away by the hormonal tides of the normal organism in its natural environment. The antiestrogen U-11, 555A, a diphenylindene derivative, made by the Upjohn Company, inhibits oviposition for several days in laboratory-held quail (C. coturnix) (McEvoy and Wentworth, ms.). This and related compounds, except for frank estrogenic agents, were the most potent oral mammalian antifertility agents reported up to 1963 (Duncan and Lyster, 1963).

Various dietary deficiencies and feed additives accidentally or purposefully included in poultry rations have been shown to depress the production of eggs. As we have already mentioned for males, dietary deficiencies are impossible to maintain in wild populations. Treatment of blackhead disease in poultry with sulfanilamide yields solf-shelled eggs that cannot hatch (Hinshaw and McNeil, 1943).

Similarly when the fungicide Arasan (tetramethylthuiramdisulfide), which is often used to protect seed, finds its way into the feed of laying chickens at 100 p.p.m., calcium metabolism is affected and soft-shelled eggs are produced (Swanson et al., 1956). Nicarbazin (Weiss et al., 1960) and glycarbylamide (Polin et al., 1961) used in the control of coccidiosis in chickens have an adverse effect on fecundity, but none of these drugs has longlasting effects.

Elder in 1964 screened two anticholesterole compounds (SC-12937 and SC-11952) to see whether they might interfere with yolk formation in the rock dove (Columbia livia). His results were spectacular. When administered for 15 days at 0.1 percent in the diet, there was complete inhibition of ovulation for 3 months and very gradual recovery over a period of several months. We have confirmed this potency in quail. These hypocholesterolemic agents seem to be the mose potent female gametocides available to date for the control of overpopulations of birds. They are new and more research is needed on their possible side effects, not to mention on the economics of their industrial production and techniques of selective administration.

Most diseases affect wildlife populations through biotic decimation. Newcastle disease virus (NDV), however, acts as a biogenetic decimator--temporary inhibition of egg laying occurs in the affected birds. The disease is almost universal among chickens, and most flocks are vaccinated against it before the chickens reach sexual maturity. Many species of wild birds, especially those in contact with poultry, are susceptible to Newcastle disease (Brandley, 1959) as shown by serum titer. It can be hypothesized that an isolated breeding colony of birds, clean and not yet immune to some strain of NDV, could be artificially infected just prior to the egg-laying season and rendered sterile for that season. Most other virological approaches to population control would seem to be fraught with hazards of great seriousness.

Embryocides

Interference with the spontaneous process of embryological development or interference with the biological conditions that sustain the life of the embryo is the most certain kind of biogenetic control. A gametocide is a pirate on the high seas; an embryocide is a practical buccaneer who lays in wait at the narrows. The embryo is surer prey than the gamete and the trade routes are best left undisturbed.

Up to this point we have been concerned with gametogenesis, an evolutionary conservative process seemingly similar in mammal, bird, and fish and virtually identical within genera, families, and orders. There is little opportunity for selectivity in attacking a conservative characteristic. But in embryogenesis and in the lifelines that nurture the embryo, there is great diversity even between closely related species. Selective control is made easier by distinguishing between a placenta and an eggshell, between a zonary placenta and a discoidal placenta, between holoblastic and meroblastic yolk cleavage, between parental dependence and independence. Turn off the incubator to kill the sparrow egg; turn it on to kill the trout egg.

In mammals, abortions or resorptions of embryos and fetuses occur spontaneously and can be induced in several ways. Medical and veterinary abortifacients are available on the shelf. Techniques for their administration to wildlife have been and are being worked out by Balser (1964) at Denver.

Landy (1962) and Coppinger (1962) of the Massachusetts unit have reviewed the physiological inhibition of embryogenesis and embryo sustentation in birds.

In chickens a great many drugs and feed contaminants have a statistically noticeable effect on hatchability of eggs. Gossypol in crude cottonseed oil or meal was found to reduce hatchability by Bird (1956). The oil of the Java olive and cyclopropene fatty acids found in many malvaceous plants (Sterculi foetida) suppress hatchability (Schneider et al., 1961). Any of the nutritional or pharmacological agents that affect quality of yolk, albumen, or shell tend to depress hatchability. We have already mentioned the fungicide Arasan causing the production of soft-shelled eggs that will not sustain embryos. For one reason or another scores of these candidate compounds have been eliminated from our screening tests with the quail; they are not available commercially, or they are too expensive to produce, or they are apparently detoxified, or, as with

Arasan, have a taste disagreeable to the bird (Arasan is actually used as a bird repellent!). Elder (1964), working with the pigeon, reported parallel experience.

Certain genetic factors that come together at fertilization are destined to be lethal to the embryo. Lethal genes in poultry and the curious phenocopies have been enumerated by Landauer (1954) and additional ones are being discovered each year. One would expect that natural selection would weed out these genes, or phenocopies, from natural populations, but that they must exist is shown by the production of "sterile" eggs by the dickcissel (Spiza americana) (Long, 1963) and perocephaly in the common grackle (Quiscalus quiscula) and mockingbird (Mimus polyglottos) (Wetherbee, 1958).

The induction of lethal mutations by ionizing irradiation is well known and is a much more feasible (if also academic) approach to the use of gamma irradiation in vertebrate pest control than attempted radiation castration.

The direct lethal radiosensitivity of avian embryos has been shown by Wetherbee et al. (ms.) to vary according to the embryonic age at exposure. A dose of 900 roentgens is lethal to 100 percent of quail embryos exposed at 1 to 7 days of age. About 50 percent die if exposed at that same level at 7 to 12 days of age whereas older embryos are much less sensitive. Pigeon eggs are a little more sensitive at all stages of incubation. But irradiation exposure of eggs for direct kill is quite impractical when actually the same end could be achieved with a hammer!

A slight improvement over the hammer was the use of emulsified oils, sprayed over the eggs of the herring gull in Maine and Massachusetts by the U.S. Fish and Wildlife Service from 1934 to 1953. This pioneer embryocidal program was a move in the right direction, but economical and sophisticated methods and tools had not been developed at that time.

We have recently published a paper (Wetherbee et al., 1964) that reports the embryocidal activity of Sudan Black B in birds. Almost all fertile eggs laid by females fed an acute dose of Sudan Black B (as little as 500 mg. per kilogram body weight) failed to hatch. This dye was shown to have no deleterious effects on adult birds, in fact an LD-50 could not even be demonstrated at extremely high levels, using both acute and chronic toxicity procedures. After a single dose of 500 mg. per kilogram, embryos in 93 percent of all eggs laid by 20 female quail for the ensuing 10 days died (significantly different from the experimental control group). The compound was found to be harmless to mice and to have no effect on the viability of mouse embryos. The dye is exerted transovarianly into the egg yolks of the immediate next 7 days' lay, after which time more dye must be ingested to maintain continued laying of affected eggs. The likelihood of secondary effects of Sudan Black B on predatory birds eating the dyed eggs is remote, as only a small fraction of the low dose ingested finds its way to the yolk; most passes out the digestive tract. Males are not affected. Field tests made by R. P. Coppinger at the Massachusetts unit indicated that this inexpensive compound was acceptable to herring gulls and met all our expectations as an embryocide, based on our experience in the laboratory.

SUMMARY

Most conflicts between man and vertebrates are directly avoidable. When the problem is not avoidable, local changes in the habitat result in diminished pressure from the nuisance. Removing the ecological requirements in short supply of the problem species is generally superior to introducing ecological intolerances. Under extraordinary conditions actual reduction of the vertebrate's population over its entire range can probably be achieved through newly developed birth-control techniques. Three types of chemosterilants are available: Male sterilants, female sterilants, and embryocides. The compounds of greatest practical utility at this time are (1) Spermatocide, T.E.M., (2) spermatocidal alkane sulfonic esters, (3) estrogen, D.E.S. (for certain mammals), (4) antiestrogen, U-11, 555A, (5) oöcide, SC-12937, and (6) embryocide, Sudan Black B.

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BIOLOGICAL CONTROL OF ANIMAL PARASITES

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The term "biological control" as here used means the employment of any naturally occurring phenomenon manifested by living things that affects the incidence of parasitism or the response incited in the host by the presence of parasites. The nature of the process initiating the occurrence of the biological phenomenon is of no consequence as long as the process immediately preceding the alteration of the degree of parasitism is biological and something other than death.

The term "animal parasite" is here used as meaning any organism of the animal kingdom that lives in or on another organism at the expense of the latter. I am limiting my discussion to the nonarthropod parasites of animals of importance in agriculture.

The purposeful use of biological phenomena to control animal parasites is not easy. In the eyes of Nature the parasites we would seek to destroy probably are as cherished as are the hosts we seek to preserve. Furthermore, forms of biological regulation are going on constantly in all natural ecological systems, and any species must, to a considerable extent, be a product of its progenitors' responses to situations not too unlike some of those we might wish to use. Parasites throughout the ages have become accustomed to certain types of adversity and have developed means of coping with them. It is unlikely that we shall baffle Nature by brandishing weapons that she has been wielding for a billion years. But with sufficient skill we may enlist her cooperation to help achieve reasonable objectives.

Our demands for enormous production of animals, the incredible ease with which we traverse natural barriers, and our almost complete disregard of the operation of natural selection all tend to favor parasitism. We have, of course, developed measures aimed at offsetting this. Some of the most successful involve the use of chemicals foreign to natural processes.

The disadvantages and limitations of chemical control have received much attention. Nature sometimes forewarns us of some of these limitations if we are attentive. For example, we should have suspected many years ago that the coccidia would probably rather quickly develop tolerances to drugs meeting the other requirements of acceptable coccidiostats. These parasites have been extremely mutable in nature. Species belonging to the two genera, both of which are of importance in our domestic animals, parasitize organisms ranging from flatworms to man. A recent catalog lists 562 species of the genus Eimeria alone (1). In contrast to this, another genus of protozoan parasites, Histomonas, belonging to a group with an evolutionary history possibly longer than that of the coccidia, is today represented by only two known species (2). The definitive hosts of both of these are gallinaceous birds. One of these two species, Histomonas meleagridis, causes a serious disease of turkeys, chickens, and certain game birds. The first two drugs that were really effective in the control of Histomonas were marketed about 1950 (3). They can still be used to aid in the control of this relatively immutable parasite.

Because some parasites can adapt to unfavorable conditions, it may become necessary to develop and utilize biological control measures or forever be committed to a continuing search for new drugs. Some of the time-tested natural procedures that operate to maintain a balance within nature, although difficult to come by, may not lose their effectiveness as rapidly as manmade ones.

To establish guidelines as to where to seek means of biological control that could possible be fruitful, we may consider, categorically at first, how the parasites of domestic animals get from one host to another. About 8 percent are transmitted primarily or exclusively by contact or by mobile stages of arthropods. About 92 percent are acquired by the host through contact with the substratum, which is usually the soil (4). Intermediate hosts or other vectors on or in the soil or the vegetation or water overlying it may be involved.

Obviously we may direct our attack on any given parasite at those stages within the body of the vertebrate host or at those stages associated with vectors or the substratum, or, of course, at both.

The principal means of biological control of parasites that operate within the body of the host are as follows: (1) Immune responses, broadly classified as natural immunity, active acquired immunity, and passive immunity and (2) the existence of conditions unfavorable to the establishment, development, or propagation of the parasite because (a) the host has not yet developed all of attributes essential to the welfare of the parasite or (b) some other parasite or some physiological disturbance has created conditions not compatible with the normal host-parasite relationship.

It is clearly impossible to elaborate on all phases of biological control of parasites. Natural immunity within a given host species can often be enhanced by selective breeding, but all too frequently it is lowered as the attention of the grower is focused on conformation, a more favorable feed conversion ratio, or some other feature.

Active acquired immunity to internal parasites has received a great deal of attention in recent decades, and it is perhaps in this area that the greatest strides have been made. A substantial part of each of several recent reviews has been devoted to the accomplishments and the literature in this field (5, 6, 7). However, even these reviews have usually dealt only with certain groups of parasites because of fundamental differences in their life histories, potentialities as antigens, and other factors. For example, protozoan parasites multiply within an individual, whereas helminths do not. Some parasites migrate extensively in the host, but others are known only in very restricted sites. Any such differences as these, and there are many, serve to make the use of potential immunological responses very complex.

In nature, passive immunity is imparted to the young of a host species through the placental circulation, the milk or colostrum, or the yolk of eggs. Obviously this area of biological control has interesting possibilities, too complex to detail here.

At present, little practical use is envisioned for employing the principle of curtailing parasitism by preventing the host's development of attributes essential to the welfare of the parasite. These attributes usually contribute also to the welfare of the host, although there are probably exceptions. For example, the fate of a parasite in the gnotobiotic animal is often quite unlike that in the conventional host (8, 9, 10). There can be many reasons. This field holds much of interest for the researcher, but little as yet for the grower.

I mentioned earlier that under natural conditions the course of a parasitism is sometimes affected by the presence of other organisms or by physiological disturbances. As might be supposed, most physiological disturbances that are unfavorable to the parasite are also unfavorable to the host if they persist. However, in many instances the success of a parasite depends on the careful timing of the progress of its stages in the host, and this timing can depend on the secretion of certain enzymes, the rate of passage of material through the digestive tract, and other processes related to feeding schedules or other activities controlled by management practices.

Intentionally introducting or encouraging the proliferation of other organisms to combat a specific parasitism may be only of theoretical interest, at least at present. To establish harmless organisms in a given region and to keep them there in sufficient numbers to have a predictable effect on a specific parasite has not proven to be easy. Possibly this is because we do not yet know well enough the circumstances that favor their proliferation.

For purposes of orientation, it may be useful to outline categorically the possible approaches to the biological control of parasites outside the body of the host and to consider for each some of the means operative in nature. These approaches include (1) the partial or complete destruction of potentially infective stages of the parasite as a result of (a) predation, (b) hyperparasitism, and (c) depletion of stored energy resources; (2) the partial or complete elimination or exclusion of important or essential vectors through agencies similar to those enumerated above; and (3) the partial or complete elimination of other biological influences that favor the persistence of a parasite or enhance its chances of being acquired by the host.

As indicated previously, about 92 percent of the parasites of our domestic animals are acquired through contract with the soil or its appurtenances. Both are vast and extremely complex, as well as varying greatly from region to region or even from place to place in a relatively restricted area. Moreover, Nature does not recognize the boundaries of man's arbitrary categories. Furthermore, the protective devices employed by the developmental stages of parasites vary widely in structure, chemical composition, and effect on the parasite's ability to respond to change in the environment or the necessity for its making a response. Consequently, I shall select as examples certain situations as they occur in nature, and point out some of the areas of opportunity for biological control, and at the same time, I hope, convey some concept of the difficulties we encounter.

Many of the protozoan parasites and a few of the helminths are transmitted directly from one vertebrate host to another by arthropods, and no stage of the parasite resides in or on the soil (4). Discussions of the control of arthropod vectors, whether a mosquito, blackfly, midge, or tick, I shall leave to the entomologists.

Little is known concerning the destruction of protozoan cysts in nature by biological means. In closed systems in the laboratory, such cysts are often destroyed by the unchecked growth of bacteria or molds or consumed by organisms such as rotifiers, small crustacea, and insect larvae. Even the relatively resistant oöcysts of at least some species of coccidia are rapidly destroyed by some molds. Freshly passed rabbit droppings kept in tightly stoppered test tubes at 4° C. have been observed to become overgrown with mold in as little as 4 to 6 days. Hyphae also penetrated the pellets. On examination, only empty oöcyst shells or shells containing a sundry assortment of globules instead of protoplasts remained as evidence of the myriads of oöcysts originally present. The results of subsequent tests were not always the same, but neither were the molds (11). The problem needs study.

But we must not suppose that what occurs so conspicuously in a closed system can be made to operate to an appreciably greater degree on the soil than is occurring without our intervention. From time to time, Brain (12) and others have reviewed the abundant literature concerning the importance of antibiotics and other forms of biological antagonism under natural conditions in the soil. When such antagonisms do occur under soil conditions, their effects are likely to be highly localized and quite transitory. To make some of them otherwise seems presently out of reach. Some do afford considerable promise, especially if we consider that the deposition of potentially infective stages of parasites is also discontinuous with regard to both time and space.

From the moment a cow discharges its feces, populations from at least three ecological sources start to mingle competitively for the most part. There are those organisms passed as part of the manure, those of the soil, and those deposited by aerial creatures attracted to the newly found situation. Physical, chemical and biological factors all start changing, almost immediately. An equilibrium may not be reached until long after the fecal pad has disappeared. What has happened to the parasites? Many, but usually not all, have died or been destroyed. Darwinism in a teacup! Sometimes predaceous fungi have been at work, here trapping, there entangling, and elsewhere, like the vulture of Prometheus, gnawing at the vitals of the young parasites (13, 14). It is quite likely that some parasites succumb to actual infections of bacteria or viruses quite specific for them.

Recently scientists of the U.S. Dept. of Agric., Agricultural Research Service found that ascarid worms in the gut of swine may be infected with an unidentified species of Pseudomonas, and that as the evidence of such infections increased, the population of ascarids in the animal was smaller than otherwise might be expected (15). The pig probably acquired the pseudomonads from the soil, although the infection of the worms probably occurred in the definitive host.

Scientists at the Beltsville Parasitological Laboratory have identified from fecal pads of cattle, and the soil beneath or nearby, organisms representing almost a dozen phyla of the animal kingdom, quite in addition to the myriads of plant organisms. Not all have an adverse effect on the spread of parasites. For example, the larvae of some parasitic helminths migrate onto and take advantage of the remarkable spore-scattering mechanism of fungi of the genus Pilobolus. In one instance, studied and recorded by Robinson in England (16), the larvae are those of Dictyocaulus viviparus, the cattle lungworm. Following the explosive rupture of the sporangium, larvae were recovered from dishes placed as much as 10 feet from the fecal pad on which the fungus was growing.

Scientists with the U.S. Department of Agriculture in Georgia have recently found the same mechanism to operate in the dissemination of larvae of certain other parasitic nematodes (17). It is probably very common. It affords the young parasites at least four advantages: (1) It removes them from the area of extremely severe competition; (2) it increases by a hundredfold or more the grazing area over which they are dispersed; (3) it further increases their chances of being ingested by depositing them on relatively clean forage, as opposed to having to await their fate at sites that grazing animals usually avoid; and (4) it accomplishes all these with minimal expenditure of the precious food reserves so desperately needed for later use.

To be able to curtail such a natural device as this should aid in the control of some parasites.

Among the many inhabitants or frequent visitors of communities, such as we have noted, are several that serve as intermediate hosts, or vectors of other types, for many of our most common parasites. Methods of biological control of any such vectors might contribute toward the control of some parasites. Flukes, for example, require appropriate snails as intermediate hosts. Biological control of snails may vary from the simple expedient of rearing ducks or geese in the pastures ranged by susceptible vertebrate hosts to the more refined, but possibly no more effective, device of replacing populations of unwanted snails with species not known to be harmful (18, 19), or the still more sophisticated method of using the larvae of marsh flies to kill the snails (20).

As I have previously indicated, if a parasite is controlled by the exclusion or elimination of an important or essential vector, this by my definition is biological control, regardless of the nature of the means used against the vector. Blackhead, or histomoniasis, a disease of gallinaceous birds, almost destroyed the turkey industry in America half a century ago, and has become troublesome in chickens of some recently developed breeds. It is caused by a protozoan, Histomonas meleagridis, mentioned earlier as a relatively immutable parasite. Itself a very fragile organism, it gets from bird to bird through the sturdy eggs of a small nematode, which also resides in the ceca of gallinaceous birds, and is Heterakis gallinarum, the common cecal worm. But sturdy as these cecal worm eggs may be and able to survive in soil for 2 or more years under appropriate conditions (21, 22), the eggs themselves lack the means of getting back into the bird, except as they may be picked up by accident. This is a precarious arrangement for an organism that produces eggs in such small numbers, as by the hundreds (23), to infect creatures that in the evolutionary past were never crowded and probably migrated to new feeding grounds before the eggs voided in a given area had become infective through embryonation.

How a parasite with the reproductive potential of *Heterakis* could have survived to be a contemporary of man and his domestic birds seems not to have distributed parasitologists for several decades, probably because a plausible life cycle could draw that satisfied the requirements of transmission under experimental conditions and might conceivably be adequate under the crowded conditions employed in modern poultry rearing (24). There were plenty of inconsistencies or evidences of that intriguing revelation we so often await: "There's something about this I haven't told you yet."

Then came a discovery. The ubiquitous earthworm, long suspect, was found to be involved in a very important way (25). The *Heterakis* eggs that it swallows during the process of feeding are *not* destroyed nor do they usually pass uneventfully through the worm to repose in its castings. They hatch, liberating the larvae that then migrate to and lodge in various places, such as tissues or coelomic cavities, of the earthworm and survive for weeks, months, perhaps even longer. They escape the harsh action of dehydration, irradiation, extremes of temperature, and attack by predators. The earthworm protects them and concentrates them until many hundreds may sometimes be present in one large *Lumbricus*, and it provides the all-important motive for their ingestion by the bird (26). Several other invertebrates may do all or some of these things (27, 28, 29). So far as we know, none does it so frequently or so well as do our friends the earthworms.

What measures of biological control we may take against the histomonad is now unclear. To attack only the histomonad requires that our attack be directed at stages within the body of the bird. This suggests immunological methods or, perhaps, the introduction of antagonistic organisms, a device that occurs even in this instance in nature (30, but that is difficult to control. Both approaches are being studied, but at this time the grower must still rely on the use of drugs if circumstances permit.

We might attempt elimination of the cecal worm, parasite of little economic importance apart from its role as a vector. To date, chemical control, although only partially satisfactory (31, 32), would probably have to be employed, along with management methods, to achieve the complete, temporary elimination of cecal worms.

Earthworms can be *excluded* from small poultry yards temporarily by various devices (33). No one would seriously suggest their eradication because of their important role in nature. I suspect that any earnest attempt to do so on a large scale would touch off a holocaust, beside which the tumult that surrounded "Silent Spring" would seem but as the gentle murmur of the leaves upon a summer's night.

I hope I have not conveyed the impression that those of us who believe in the merits of biological control as a means of combating parasitism are defending a hopeless cause. I must admit, however, that we made a tardy start. In this respect, we are like the small boy being questioned by an adult passing nearby what the score was in their sandlot game of baseball.

"Sixty-seven to nothing, their favor," he gasped between fielding efforts. "You're getting beat pretty badly, aren't you?" the sympathetic onlooker queried. To which the lad replied, "Naw, we hain't had our bats yet."

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PEST CONTROL BY GENETIC MEANS

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Previously in this symposium we considered pest control by biological means. Pest control by genetic means is in actuality also a form of biological control. In this form of control the characteristics of the host that condition resistance to a pest are heritable. The virulence of a parasitic organism or its ability to attack a host, however, also is under genetic control. Pest control by genetic means therefore must involve determination of the interaction between the genetic systems of the host and the parasite, commonly called host-parasite interactions.

Natural selection has been an important factor in the evolution of all economic species, both before and after domestication. Major among the selective pressures that were associated with survival in the wild were ravages by pests. Characters associated with survival are not necessarily those that make a domesticated species useful to man; nevertheless, many characters that contribute to survival in wild species also are associated with quality and quantity of productivity of these same species when domesticated. Such is the case with genetic resistance to pests.

Pest control by genetic means is undoubtedly one of the oldest forms of biological control that man has pursued intensively in his attempts to tilt the "balance of nature" in his favor. As a consequence of the famine in Ireland in the middle of the 19th century, varieties of potatoes resistant to late blight were developed prior to 1900. Resistance to insects was recorded as early as 1860, with the discovery that American rootstocks of grape were resistant to phylloxera. One of the earliest recorded instances of development of varieties resistant to insects, however, occurred with the breeding of wheat varieties resistant to the Hessian fly in the early 1920's. Barley varieties resistant to the cereal cyst nematode were developed in Europe also in the early 1920's.

Although differences in animal resistance to pests, such as resistance of zebu cattle to the Texas fever tick, have been reported, the cost of exposing large numbers of animals has precluded the possibility of active breeding programs to exploit such resistance.

Breeding of genetic resistance in domestic species is one of the most economical methods of combating damage and destruction by pests. In most cases, this type of control is not permanent. The ability of parasitic organisms to adapt themselves through natural selection to previously resistant hosts necessitates constant alertness for new attacks and requires continuing research programs to maintain resistance.

ADVANCES AND CHALLENGES IN THE CONTROL OF PLANT DISEASES THROUGH BREEDING

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The development of crop varieties that resist, tolerate, or escape the attack of pathogenic organisms or viruses has been a prominent phase of scientific agricultural development. A multitude of such accomplishments, old and new, have been built into the structure of modern agricultural production. Many of these successes are time tested and solid and encourage effort to extend such gains to all diseases that threaten the plants we value or must produce. Some advances have been of ephemeral value and require costly repetition of effort, because we have not possessed the requisite knowledge or wisdom to do a more permanent, better job. It will be possible to review only a few of the problems and accomplishments that mark the path of progress toward plant disease control through breeding.

My field of first-hand knowledge and experience is that of disease resistance of the field crops. For convenience and security, and not because I consider it unique or requiring special attention, I will draw heavily on this area to develop certain ideas on disease resistance.

TIME-TESTED VICTORIES OVER PLANT DISEASES

The breeding of disease-resistant crop plants has been going on for a long time. Even in prehistoric times, one really smashing success was achieved. This was the development of maize essentially resistant to its leaf rust disease caused by Puccinia sorghi. This disease has been well under control in field corn during the entire history of its culture in the Corn Belt of the United States. There is no record of sweeping epidemics of this rust, only light infections that have been common and widespread on open-pollinated and hybrid corn. For reasons still not completely understood, devastating epidemics were unable to build up on most corns, although they appeared to be susceptible when inoculated. However, the fact that the environment is often favorable to this rust is evidenced by severe infections that have been observed on sweet corn and certain dent corn inbreds with high susceptibility. Apparently, as proposed by van der Plank (34), corn possesses a generalized and stable resistance to leaf rust. This "generalized" and permanent type of resistance of corn draws the jealous attention of those of us who have fought the battle against rust races of the small grains with some wins and some losses. We shall return to consider the possibilities in such resistance that may provide the clue to building better resistance to many important diseases.

Another disease resistance that has been around for a long time and has served well is field resistance in the potato to the late blight disease caused by Phytophthora infestans. Breeding for blight resistance began over 100 years ago in Europe after the devastating epidemics of the 1840's and the Irish potato famine of 1845 (2). Good varieties were developed by 1900 with moderate resistance, enough to greatly reduce losses and to render control by fungicides more effective. Such resistance has formed the basis for modern breeding for polygenic field resistance, which has remained stable through the years, although not of a high or immune type.

Possibly the most sensational work on disease resistance of all time is that of the pioneer workers against the wilt diseases caused by forms of the fungus Fusarium oxysporum. These diseases were devastating on a wide array of major crops, ranging from flax to banana. Because the causal fungi reside and persist in the soil, they are able to attack persistently and with increasing severity after the soil becomes infested.

W. A. Orton of the U.S. Department of Agriculture conceived the idea of selecting individual plants that survived on wilt-infested soil, although the cause of the disease was not then known nor were the principles of pure line selection or Mendelian inheritance. By 1899, he had selected wilt-resistant lines of cotton from infested fields in South Carolina and within 10 years had released a group of named varieties (6).

The flax crop of the United States made its "last stand" in the middle Northwestern States in the first decade of the century. It continuously had been forced to move westward from the Atlantic States to avoid "flax-sick" soils, where the crop had been grown for a few years (8). The crop was saved by the pure line-resistant selections of H. L. Bolley of North Dakota made during 1902-12 and distributed from 1908 to 1925.

I witnessed the end of the struggle to grow wilt-susceptible flax in eastern South Dakota about 1910. I recall a large field on my uncle's farm, where the flax crop had made normal growth and was in full flower. But on this day every stalk was flaccid and the flowers hung limp. This was about the end of flax growing in that region until Bolley's resistant selections brought it back some years later. Wilt resistance became a must for crops that were attacked by the fusarium wilt fungus. Today the cabbage-, pea-, tomato-, and melon-growing industries in many areas owe their existence to the development of fusarium wilt-resistant varieties.

Sugarcane mosaic, known in Asia in the past century, is believed to have been introduced into the Southern United States about 1914. The disease spread rapidly and by 1926 had brought the industry to near ruin. Production in Louisiana of over 200,000 tons had been reduced to 47,000. Losses to the industry amounted to $100 million annually (3). A breeding project was established at Canal Point, Fla., by the U.S. Department of Agriculture, under the leadership of E. W. Brandes, to find or breed mosaic-resistant replacements for the old varieties D74 and Louisiana Purple. Resistance derived from the wild sugarcane Saccharum spontaneum was combined in resistant improved types by crosses with commercial varieties of S. officinarum (6). Within 10 years, following the collapse of sugarcane production in 1926, planters and sugar factories were back in business with resistant varieties that were far better adapted and more productive than previous varieties ever had been (3). This was an early and impressive demonstration that crossing of genetically diverse parents, as enforced by breeding for disease resistance in this instance, may greatly expand the scope of possibility for improvement in adaptation and productivity of crop varieties.

Strangely enough, another virus disease, curly top of sugarbeet, brought another sugar industry to near bankruptcy in the western irrigated areas of the United States. Eubanks, Carsner, and D. A. Pack produced the first partially resistant variety, U.S. No. 1, in 1929 by mass-selecting resistant plants from commercial sugarbeet stocks (5). It soon was followed by more completely resistant stocks, U.S. 33 and 34, selected from U.S. 1. Under conditions of curly top exposure, U.S. 34 produced over 10 tons, compared with only 2 to 3 tons per acre by the old commercial brands. The breeders of curly top-resistant varieties scored a spectacular success that saved the sugarbeet crop for large areas in the Western United States.

These contributions to plant disease control by resistance breeding are presented to represent the multitude of equally significant accomplishments in disease resistance that have been built into the structure of modern agricultural production and have proved their stability and value. These successes are time tested and solid and can only encourage greater research and breeding effort to contain those important diseases still resisting control or not being vigorously attacked.

MORE RECENT CONTRIBUTIONS TO DISEASE RESISTANCE

Soybean, a new crop long escaping drastic attack by diseases, now suffers from an array of important diseases, among them a recently destructive root rot disease caused by Phytophthora megasperma var. sojae. Fortunately high resistance was found in relatively good types, such as the old variety Mukden, but the widely grown and productive varieties were highly susceptible. Breeders and pathologists of the U.S. Department of Agriculture and several soybean-producing States initiated a crash program in 1957 to transfer the monogenic resistance of Mukden to the commercial varieties by backcrossing. Only 6 years later, in 1963, resistant lines essentially isogenic with four popular commercial varieties, Harosoy, Hawkeye, Lindarin and Clark, were cooperatively released in the States concerned, followed by a fifth variety in 1964 (22). This I believe establishes a record of timely and rapid genetic manipulation of a major crop to meet a threatening production hazard.

Open-pollinated corn in the Corn Belt of the United States historically has not been beset by aerially distributed diseases developing in epidemic form. However, severe epidemics of the northern corn leaf blight (Helminthosporium turcicum) began to occur soon after the establishment of susceptible varieties of hybrid corn during 1940-50. Early onset of the disease 2 to 3 weeks after silking may result in severe losses (32). Field resistance to H. turcicum has been found, studied genetically, and transferred to commercial hybrids that are widely available and extensively used (13). This has been a difficult and praiseworthy job, with a polygenic, hard-to-handle resistance, by cooperating State, Federal, and private agencies.

I have saved until last a discussion of the efforts of breeders and pathologists against the rust and smut diseases, because the types of resistance used have been important in limiting the results achieved. However, much of the faultfinding with the past pioneering efforts is attributable to hindsight and is akin to "Monday morning quarterbacking." But history has been repeating itself so often that now there can be little doubt of needed redirection of both research and breeding. Lest it appear that I see only the hole in the rust-resistant doughnut, I wish to review a few of the many accomplishments that have brought immense benefits.

Stem rust (Puccinia graminis) of small grains, has been one of the most elusive diseases that breeders have attempted to control, but even here the economic gains have been tremendous although transient. Craigie (7) calculated the gain in yield and income from use of stem rust-resistant varieties in Manitoba and Saskatchewan, Canada, from 1938, when they were first intensively grown, to 1943. The calculations were based on extensive and dependable yield comparisons of the resistant varieties versus the susceptible Marquis. Through this 5-year period, the average gain was over $27 million annually. This compares with an alltime total expenditure on rust research and plant breeding of less than $2 million in Canada.

The spring wheat Selkirk bred by the Canadian Department of Agriculture at Winnipeg, Canada, for resistance to race 15B of stem rust was released in 1953, and to the present it has been by far the predominant variety in both Canada and the spring wheat area of the United States. Through this 11-year period it has maintained its resistance in the field in such years as 1962, when much of the crop was late and susceptible varieties, such as Red Bobs, were nearly destroyed by stem rust. Financial gains thus far from this one variety in Canada and the United States probably would extend to multiples of $100 million.

Extreme difficulty has been experienced in maintaining oat varieties resistant to crown rust (Puccinia coronata avenae) in the entire oat-producing area of the United States. Nevertheless, tremendous losses have been prevented by the breeding of a number of resistant varieties. Accurate measure of gain from growing the resistant variety Clintland, from Purdue University and the U.S. Department of Agriculture, was possible in Indiana in 1957 during the last severe crown rust epidemic. Clintland and other resistant varieties in small acreage were grown on 67 percent of the State oat acreage. Since Clintland is essentially isogenic to Clinton, a susceptible older variety, field-plot comparisons over the State gave an accurate measure of the relative yields. Gains, thus calculated at a value of 62 cents per bushel, amounted to about 9.5 million bushels, worth nearly $6 million. Here, in a small State, in a single year, on one crop, the measured gain from resistance to one disease exceeded several times the estimated investment for all crop-disease research and breeding work in Indiana by the State and Federal Governments. In 1957, Clintland was probably the most widely grown oat in other Corn Belt States, where total gains from its resistance were many times those measured in Indiana.

The breeding for resistance to bunt of wheat caused by Tilletia spp. in the Pacific Northwest has made possible the maintenance of wheat growing in dry areas where bunt spores could persist in the soil and seed treatments were not effective. A series of resistant varieties have been produced first by E. F. Gaines, of Washington, who released the well-known Ridit in 1924 and Albit in 1927. As required to control new races of bunt, these have been followed by a series of improved varieties, the most recent of which have been Elmar (1949), Omar (1955), and Gaines (1962).

CHANGING RACES

Satisfaction in this review of victories in the breeding for disease resistance is marred by some serious defeats. These defeats have come about largely through the development of physiologic races of the pathogens causing several of the most important diseases of our major crops. The depredations of such races are too numerous to mention more than a few examples.

Races of stem rust of wheat, oats, and barley are probably the most notorious offenders. First, race 56 emerged to attack the first resistant wheat variety Ceres. Then race 15B arose, which could attack the durum wheats and the bread wheats Thatcher, Lee, Regent, Renown, Apex, and Redman, all having good previous records for resistance. The variety Selkirk, released in 1953 by the Canadian Department of Agriculture, is resistant to race 15B. However "biotypes" of races 15B and 29 have been found that attack it in the seedling stage. It is noteworthy that these new "biotypes" have not become destructive on Selkirk through a 10-year period, although they must have repeatedly occurred in the vast acreage of this variety.

Stem rust resistance on oats (P. graminis f. sp. avenae) has been particularly ephemeral. The resistance of Clinton, conditioned by gene D, was overcome by destructive epidemics of race 7. The resistance of Tama and Vicland (gene A) gave way before race 8. Varieties now carrying stem- rust-resistance genes A, B, and D, those principally used to breed the present varieties, are completely susceptible to the newer races 6A and 6AF. Thus, we have no oat variety at present that is resistant to all well-distributed races.

The crown rust of oats (P. coronata avenae) like stem rust repeatedly has been able to vary its virulence sufficiently to thwart the best efforts of breeders. Varieties such as Clintland possessing the LL gene pair from "Landhafer" are thoroughly susceptible to predominant strains of the rust. At present there is no commercial oat variety that is highly resistant to existing races of crown rust in North America.

Prevalent races of stripe (*P. striiformis*) in both Europe and the Americas have changed repeatedly to render new resistant wheat and barley varieties susceptible.

Thus far, all wheat varieties bred in the United States for seedling resistance to powdery mildew (*Erysiphe graminis* f. sp. *tritici*) have ultimately been attacked by races of that parasite. However, some wheats susceptible in the seedling stage have shown different levels of mature-plant resistance in the field. Such resistances have remained at a useful or even high level over a period of years, as in the variety Knox, distributed in 1953, which hopefully may continue to provide resistance against all races of the pathogen.

The history of gains and losses in resistance to wheat bunt in the Pacific Northwest (16) closely parallels that for stem rust of wheat. The varieties Ridit, Albit, Rex, and Hymar, each resistant to certain races, have served to screen out and multiply races to which they are susceptible. Thus, when the excellent variety Elmar became predominant, races that could attack its parent Hymar were ready and caused devastating epidemics. Now the varieties Omar and Gaines have replaced Elmar. Thus far, they have been resistant in the field, but race T-18, which can attack Omar, is known and possibly is waiting to make a dramatic appearance.

These are a few cases out of many selected from the area of cereal disease resistance, where resistance has been nullified by the appearance of new races. In a large measure these "lost" resistances are characterized by monogenic genetic control and often but not always by localized death of host tissue as a reaction to the invading pathogen. This reaction has been called hypersensitivity by Stakman (30) and the resulting killed area a "fleck." This visible fleck or internal necrosis commonly has been associated with an ephemeral resistance, soon to be lost to new races. Such resistance has been termed racial resistance by Niederhauser et al. (19).

Contrasted with these resistances, that are soon overcome by new pathogenic races, are "generalized" types of resistances, which may not be overcome by new races. The classical example of the contrasting values of these two resistance types is found in the potato, which possess both types of resistance to late blight. The "R" genes, derived from *Solanum demissum*, condition hypersensitivity resistance to *Phytophthora infestans*. Such resistance alone, however, is of little value, as in the Kennebec variety introduced in 1948 and severely attacked by late blight in Maine in 1954. Niederhauser et al. (19) described the ineffectiveness of the "R" gene resistance in Mexico, where varieties with the "R" resistance genes in different combinations were killed by specialized races of the pathogen. However, several *Solanum demissum* clones, possessing "partial" or "field" resistance, remained green and viable and retained their resistance in succeeding years although suffering a light attack. Likewise the European varieties Alpha, Gineke, and Voran also showed field resistance. These could be successfully grown under severe blight attack in the damp summer seasons at Toluca, Mexico, with moderate spray programs.

VERTICAL VERSUS HORIZONTAL RESISTANCE

The persistent resistances having a generalized effectiveness against all races of a pathogen have been designated by a number of names, none of which is adequately meaningful. Those used most commonly include field resistance, polygenic resistance, partial resistance, generalized resistance, and tolerance. The last term implying endurance of the pathogen rather than resistance to it is quite misleading. Recently van der Plank (34) has proposed the useful terms "vertical resistance," to include those types effective against only certain races of a pathogen, and "horizontal resistance," which is equally effective against all races of a pathogen.

Vertical resistance is typified by the "R" resistances to potato late blight and the ephemeral, hypersensitivity resistances to the rust fungi. It possesses the virtues of high-level resistance, usually simple inheritance, and ease and economy of recognition in parents and hybrid progenies in breeding programs. Its serious limitations are its instability and nullification in the presence of new races of a pathogen and the fact that, when present and effective, it may obscure an underlying dangerous, supersusceptibility to any new race that arises to attack it.

Horizontal resistance is typified by the stable, polygenic resistance to late blight of potato. The one great virtue of horizontal resistance is its permanence. Its liability is its usually multigenic inheritance, making it of rare occurrence and costly to recognize and recover from hybrid progeny.

CURRENT APPROACHES TO BETTER USE OF VERTICAL RESISTANCE

One attempted approach to more successful use of monogenic, vertical resistance in the wheat rusts has been the transfer of genes from related grass genera to the genus Triticum. Some of us have held hope that resistance derived from distant wheat relatives might be more enduring than that provided by genes found occurring naturally in wheat. Such a resistance from Aegilops umbellulata was supplied by Sears (28) in the Transfer variety. No races of leaf rust (P. recondita) attacking this variety have been found in nature in North America. Samborski (27), however, produced such a virulent clone by selfing a Canadian culture of this species on the alternate host, and recently the Rockefeller Foundation (24) reported Transfer to be susceptible in the field in Argentina. Thus, this Aegilops resistance also proves to be undependable. Several wheat derivatives of Agropyron elongatum, including Agrus and Agatha with an immune reaction to leaf rust, are being intensively studied in interstate and international tests. Thus far, they have remained resistant. There is, however, no firm ground for hope that vertical resistance derived from interspecific and intergeneric crosses will provide the needed dependability of resistance. Knott and I-sun Shen (17) have recommended that continued attempts be made to provide new sources of resistance to stem rust, by hybridization of wheat with related species and genera, to supplement the relatively few vertical resistance genes now known.

The breeding of "multiline" varieties, possessing vertical resistance, has been proposed by Jensen (15) and Borlaug (1) as an approach to more stable rust resistance. Here, several vertical resistance genes are individually added to single, near isogenic lines that are then composited for commercial use, as the incidence of new races may require at any one time. This approach is based mainly on the theory that no one race will develop rapidly enough on susceptible plants surrounded by resistant plants to cause severe damage. The practical proof of the theory of disease control by multiline varieties largely remains to be provided. The method is laborious and would require most of the resources of most breeding programs and thus limit much that might otherwise be done in creating inherently better crop varieties. The method is highly conservative, restricting the breeder to older crop genotypes of proven performance. The mixture of resistance types might provide the ideal situation for breeding new races by vegetative recombination of virulence genes of the old rust races, if mechanisms of vegetative recombination operate under field conditions, as proposed by Nelson et al. (18), and Ellingboe (9). The Rockefeller Foundation (24) has announced the release of the first multiline wheat variety, Miramar 63, with resistance to both stem and stripe rust in Colombia, South America. The degree of success and permanence attained in controlling the development of rust epidemics with this first multiline variety will provide valuable guidance to future breeders.

At Purdue we have used a mature-plant vertical resistance of a polygenic type to produce effective mature-plant resistance in the soft red winter wheat varieties Knox and Vermillion, grown on about 2 million acres in the Southern and Eastern United States during most of the past decade. Their resistance, derived from Chinese C.I. 6223, has been shown by Unraw et al. (33) to be conditioned by genes on four chromosomes. Our studies have also indicated polygenic inheritance in both Chinese and Knox with segregatants in F_2 hybrid populations ranging continuously from 0 to 100 percent field infection. During 1962 to 1964, races have appeared that cause up to 30 percent infection on Knox and Vermillion as compared with 100 percent on susceptible checks. This resistance, despite its polygenic inheritance, is therefore of the hypersensitivity and vertical type. Thus, polygenic resistance cannot always be equated with horizontal resistance. However, the Chinese resistance of Knox and Vermillion has been fairly stable for a decade, and still gives protection from leaf rust in Knox, even when it is surrounded by inoculum-producing susceptible varieties. In uniform fields it may still give adequate protection from all current races.

Shay et al. (29) question using "monogenic" versus "multigenic" resistance to apple scab (Venturia inaequalis) as "becoming academic." They grant that monogenic resistance is more highly subject to nullification by new races, but report that resistance breakdown may occur in either case. Here, however, multigenic resistance to apple scab is not necessarily to be equated with horizontal resistance. They could find no logical basis for selecting a resistance genotype with a guarantee of long effective life and suggest that the only safeguards against loss of a variety from new races of V. inaequalis is the use of a many genes as possible from both the monogenic and multigenic systems.

USE OF HORIZONTAL RESISTANCE

Horizontal resistance, by definition as well as experience in some cases, is persistent or permanent and therefore is the preferred type if it is sufficiently effective. Horizontal resistance appears to result from host characters that limit the rate of infection reproduction and build-up of epidemics by the pathogenes rather than from host characters bringing about cellular, host-parasite interactions that are detrimental or lethal to pathogens and often recognized by host hypersensitivity. Thus, when for any reason, such as artificial epidemics, the pathogen becomes abundant, horizontal resistance appears at a disadvantage, whereas a vertical resistance, such as hypersensitivity, may appear outstanding under such a test. Therefore, one must look further than an artificial test plot for the true value of horizontal resistance. Horizontal resistance, resulting from two or more specific host characters, may be expected to be polygenically inherited, but not all polygenic resistance is of the horizontal type.

The simplest possible kind of horizontal resistance is possessed by some two-rowed barleys against loose smut (Ustilago nuda). To infect the barley embryos, the smut spores must first gain entrance to the young pistil of the flowers when they commonly open at pollination time. The flowers of some two-row barleys, such as the English Proctor variety, remain closed at pollination time ("close-flowering") and thereby exclude the smut spores. This character results in highly adequate resistance to all races of the smut fungus. A highly dependable, yet inexpensive method, had been devised by Pederson (20) to select the close-flowering types.

In contrast to this example, horizontal resistance may result from the interaction of several host characters. Guzman (10) analyzed the nature of horizontal resistance to potato late blight referred to as "partial resistance." She found it to result from effects of the resistant host on the development of the pathogen in four ways: (1) Delayed host penetration, (2) reduced frequency of penetration, (3) delayed rate of host tissue invasion, and (4) reduced sporulation by the pathogen. These characters were measured effectively in the greenhouse to discriminate horizontally resistant from susceptible segregants in hybrid populations. Such tests were equally as effective as much more costly field tests.

The selection for leaf rust (P. recondita) resistance in our program of wheat breeding at Purdue has been largely with mature plants in the field under artificial epidemics of combined rust races. Under these conditions we have brought together mainly mature-plant resistances. The variety Dual, selected in this manner, possesses a mature plant resistance superior to any of its parents (4). It is susceptible to most races as a seedling. It appears likely that some elements of both horizontal and vertical resistance have been combined in this variety, which has maintained an effective level of field resistances during its breeding, selection, and commercial use from 1942 to the present.

Romig (25) and Romig and Caldwell (26) reported that a number of leaf rust-susceptible but "slow-rusting" winter wheats displayed resistance to stomatal penetration of mature wheat leaf blades by the rust. The rust germ tubes that failed to penetrate frequently developed deformed appressoria. Field tests indicated that leaf rust epidemics spread more slowly in plots of these varieties than in normally rusting varieties. These slow-rusting varieties appear to have at least one important host character for resistance that alone or collectively with other types may bring about an effective field resistance of the horizontal type.

Hayden (11) found Marquis wheat to become 15 to 20 times as severely infected with stem rust in the field as did the field-resistant variety Sentry when exposed to equal inoculation. This resistance of Sentry, in the hands of future breeders, may prove to be a valuable element of horizontal resistance. The Marquis wheat variety dominated the spring wheat region, where it was grown on nearly 12 million acres from 1914 to about 1930. During the 1920's, my observations in South Dakota were that it was not severely attacked by leaf rust. However the variety Kota, introduced in the 1920's, suffered the most serious leaf rust attack I have ever seen. Prior to those epidemics, leaf rust in that area was not considered to be a serious wheat disease and caused little concern. Marquis, however, is susceptible upon inoculation in the seedling stage. This record suggests that, when grown on vast and continuous areas, it may have possessed enough horizontal leaf rust resistance at maturity to prevent the development of serious epidemics. The varieties Kota, Ceres, and Thatcher, which were released to replace Marquis, were seriously attacked by leaf rust. Records in the U.S. (interstate) Uniform Spring Wheat Rust Nurseries show Marquis to have been consistently less severely attacked than Kota, Ceres, and Thatcher during the 1930's, even when surrounded by rust breeding-susceptible varieties. A study of the nature of leaf rust resistance in Marquis might well provide valuable guidance to resistance breeding.

The persistence of the stem rust resistance of Selkirk spring wheat mentioned earlier is highly encouraging. This variety has not been severely attacked in the field for the past 11 years despite the fact that race 15B3 and two biotypes of race 29 were found attacking it as far back as 1952-54. Such stem rust races must have occurred repeatedly since 1952, but have not produced damaging epidemics. Selkirk possesses the Sr6 gene for vertical stem rust resistance and some or all of the resistance of its parent Redman. Redman and other derivatives of Hope and H-44, while susceptible to race 15B as seedlings, have not shown extremely high mature-plant susceptibility as have certain durum varieties. This field resistance was reported by Peturson (21) and Stakman and Christensen (31). It has been repeatedly observed on Hope derivatives in our nurseries inoculated with different clones of race 15B. It may be possible that Selkirk combines a seedling vertical resistance, combined with a mature-plant horizontal resistance, that suppresses the multiplication of the new races that can attack it in the seedling stage. If found to be true, this would be indeed fortunate and could point the way toward breeding far more stable stem rust resistance.

Mention has been made of the successful use of a field resistance to control the northern leaf blight of corn. This resistance is expressed in restricted growth of the parasite in the host and smaller host lesions (14), and is polygenic in inheritance. These characteristics and the lack of precise host specialization of the pathogen on the resistant corn inbreds (23) suggest strongly that this resistance may be of the stable horizontal type that may not be overcome by new races.

One cannot at this time be so hopeful for the monogenic resistance to this disease recently described in corn inbred G.E. 440 and Ladyfinger popcorn (12). The monogenic inheritence, and comparatively high resistance conferred are suggestive of the vertical type of resistance. However, this resistance has been enthusiastically received as offering an easier way to breed resistant corn, and is being widely used.

A serious problem is posed concerning the method of using this resistance, which in some ways appears superior to those now in use. The problem is emphasized here because it is typical of many to be faced in the future. In view of the past uncertain and, in some cases, sad experiences in the use of monogenic vertical resistance to the rusts, smuts, potato late blight, and the powdery mildews, it would appear unwise to risk such an experience with a disease of such potential as the northern corn leaf blight of corn. The risk is unnecessary, as valuable time-tested resistance is now available. A switch to exclusive and widespread use of a resistance that in time could possibly prove to be of the vertical, or short-lived type, could result in the production of future hybrids with unstable resistance and supersusceptibility to new races.

Experience indicates that we should treasure the older, polygenic, and probably horizontal resistance, since it has a record of stability over a period of years, and use the newer, more hazardous, monogenic resistance as a supplement to it. Such a combination might give both higher resistance and stability. Such a breeding program will be the more difficult, and for the near future the more costly way, but it will be much safer and ultimately may be much more practical.

FUTURE DISEASE-RESISTANCE REQUIREMENTS

The work to be required of disease-resistance breeders and pathologists looms large for the future. Ultimately food requirements will demand all possible elimination of disease losses to the major food and feed crops. Such demand will likewise require high plant populations and the increased fertility needed to produce the necessary high yields. Already we see such diseases as powdery mildew of small grains causing increasingly frequent and heavier losses of major proportions as optimum nitrogen requirements are met and dense stands become necessary. Other foliage diseases, previously of little concern, such as Septoria tritici leaf blight of wheat, likewise become seriously destructive as culture is intensified.

Much knowledge is yet to be gained by appropriate research before we have the necessary understanding to breed for resistance to these enemies of the food crops as effectively as we must when world population presses ever more forcefully against the food supply. Stepped-up support for production research in agriculture must replace apathy from public and private agencies, which have tended to see only surpluses and little need for more efficiency in crop production. Research must be done to understand the more durable and often intricate, horizontal types of disease resistance and to test their utility. Such an increased attack on disease should not be long delayed. When the need becomes imminent, it will be too late to legislate for effective crash programs to breed more efficient crop plants, unless the appropriate research and the training of scientifically competent and agriculturally sophisticated plant pathologists and breeders have not been neglected during a passing era of localized plenty.

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CURRENT STATUS AND OPPORTUNITIES FOR THE CONTROL OF NEMATODES BY PLANT BREEDING

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Despite many advances in the control of plant-parasitic nematodes by biological or by nonbiological methods, the estimated annual losses in the United States, based upon actual trials on 18 crops, amount to nearly $400 million (81). The total annual loss for the 78 common agricultural crops may well approach $1 billion. Such heavy loss justifies expanded research in nematode control by breeding and other means.

These losses may be estimated from reduction in yields of individual plants (5, 27, 56, 90, 127), from lack of survival during summer (6), from poor stands (10), from lowered quality of produce (22, 44), or from increased susceptibility to cold injury (37). The use of low-income, nonhost crops to control nematode populations also contributes to the total crop losses. Crop damage by nematodes has been attributed to decreased fertilizer efficiency (37, 131), decreased water uptake (37), increased susceptibility to attack by pathogenic fungi and bacteria (1, 19, 70, 86, 100, 104, 105, 120), and interference with metabolic processes (37).

Not all plant-parasitic nematodes are harmful; there are at least two cases of host-plant stimulation attributable to nematode attack.

The development of plants possessing genetically controlled resistance to nematodes has been recognized as one of the most effective and economical means of reducing the losses caused by these pests, especially the root-knot nematodes. However, the appearance of physiologic races has raised the question as to whether there can ever be permanent control solely by genetic means (18). This paper deals with the problem of physiologic races and other problems in breeding for nematode resistance.

VARIABILITY IN NEMATODES

In breeding plants for resistance to any plant parasite, whether it be insect, virus, fungus, bacterium, or nematode, the plant breeder, if he is to make lasting progress, must consider the genetic variability of the parasite as well as that of the host plant. Populations of both are plastic and dynamic.

A paper prepared nearly 40 years ago by Steiner (130) presented these fundamental principles of population genetics:

(1) Nematodes prefer the host species on which their parents lived.

(2) This preference grows with each succeeding generation.

(3) Utimately the specialization may reach such a high degree that distinct new hosts of even the closest taxonomical, physiological, and chemical relationships are either not attacked or attacked very lightly.

(4) Starved nematodes will attack a host that otherwise they would completely ignore.

If expressed by a population geneticist, Steiner's principles would be:

(1) Differences and new mutations of genes and chromosomes occur in all organisms.

(2) Mutations are selectively sorted out by the environment and passed on to the surviving progenies.

(3) They are the basis for genetic changes leading to noticeable variability, to genetic drift in a given direction, and ultimately to new races.

(4) Any condition that speeds up mutation rate or increases selection pressure will automatically accelerate race development.

Nematodes possess almost infinite variability. They can infest man, animals, and plants. They can thrive in soil and in both fresh and salt water. They can withstand extremes of temperature from -271° C. to 61.3° C. (131). Some species can endure dry storage for as long as 39 years (133). Information accumulated over the past century indicates that one form or another can parasitize most crop and ornamental plants grown in the world (133).

In addition to vast and multidimensional patterns of existing variation, many nematode species reproduce sexually and thereby insure the optimum and virtually limitless potential for new genetic combinations, a distinct evolutionary advantage. Such wide diversity of germ plasm provides nematode populations with an extremely high degree of versatility to adapt rapidly to abruptly changing environments.

RACE FORMATION IN NEMATODES

Nematodes may be destroyed in large numbers, but the remaining few can rapidly build up large populations in the altered environment. Survivors of soil fumigation have been demonstrated to restore original population levels completely in one growing season (92). This high reproductive efficiency permits increased numbers of new genetic recombinants per generation to be tested against all changed conditions. The net result may be the evolution of new races in remarkably short periods. As already mentioned, any condition that speeds mutation rate or increases selection pressure will automatically accelerate race development.

Rau and Fassuliotis (106) have found evidence of genetic drift in nematode populations by using statistical means. Thus, shifts toward new race formation, and even speciation, can be shown. Additional studies in microevolution of *field* populations of nematodes are needed. Estimates of the number of organisms that give rise to the next year's population are an important parameter for rates of expected genetic drift.

Among nematologists and plant breeders, the development of physiologic races of the golden nematode, *Heterodera rostochiensis* Wollenweber, 1923, is recognized as a classic example of race formation in nematodes, and is described in the following.

Breeding studies with resistant clones of *Solanum tuberosum* L. subspecies *andigenum* (Juz. & Buk.) Hawkes were started in Holland in 1946 (71) and in England in 1952 (34). This species was probably used because it is a tetraploid that readily yields fertile hybrids with the potato, *S. tuberosum* L., which is also a tetraploid. Nine years later a physiologic race of golden nematodes was reported in England (34, 78) and another somewhat later in Peru (72). In these same experiments, *Solanum vernei* Bitter & Wittm., a diploid, maintained its full resistance (34). In Europe the latter species was not generally used until recently, probably because it is a diploid species and therefore fertile hybrids with *S. tuberosum* are difficult or impossible to obtain, or because resistance did not "inherit according to simple mechanism" (73). By 1960, at least three distinct races of the golden nematode could be distinguished in the Netherlands: Race A (the parental strain), race B_1, and race B_2 (73). In England comparable strains were called nonagressive, Duddington, and Bogshall (35). It became evident that repeatedly growing resistant varieties on the same field would not eradicate the golden nematode. Nematode populations were stabilized at a low level after 3 years of cropping with resistant varieties; the crop was not noticeably damaged (74). However, because of the buildup of resistant biotypes (21), a marked increase in nematode populations occurred after the sixth year. Similar resistance-breaking races occurred in Germany (132). At the most recent count, 12 races could be identified. The need has been expressed for a system of nomenclature akin to that used by plant pathologists, to identify the unending physiologic races that continually appear in the late blight organism and the cereal rusts.

The race problem in the golden nematode and in potato late blight organism has several striking similarities. Because the late blight problem is nearing a workable solution, certain similarities may be clues to a solution of the golden nematode problem. First, in both cases the factor for resistance came from a single species and was inherited as a single dominant gene (72). Second, additional races could be attributed to mutations at a single gene locus, a means by which the various races could be identified. Third, there seems to be an infinite number of potential races in both organisms. Unlike late blight, which spreads through the air, the golden nematode spreads very slowly in the soil. It has been estimated that nematodes seldom move more than 1 to 2 meters per year (133, 140, 146). This slow spread is vital to effective control measures. Nematodes can, of course, be spread by tillage procedures, by being carried on potatoes, bags, shipping materials, and by similar means.

The solution to the late blight problem appears to center on finding a type of resistance that protects a plant from *all* races. Such resistance found within the *S. tuberosum* species is inherited by an unknown number of multiple genes, and to date it has protected the plant against all known races of the pathogen.

In the United States resistance-breaking biotypes of the golden nematode apparently have not been found (65). However, breeders here have for nearly 10 years been actively using resistance from *S. vernei*, as well as that from *S. andigerum*. A fertile cross with *S. vernei* resulted from an unreduced gamete of the diploid *S. vernei*, combining with the reduced gamete of *S. tuberosum* to from a fertile tetraploid hybrid. Subsequent genetic studies at the diploid level indicated multigenic inheritance of resistance (42, 101).

A solution to the race problem in golden nematodes might very well be found in the use of multiple-gene resistance from *S. vernei*, coupled with known resistance from other *Solanum* species (79) to build up a multigenic system. The mathematical probability of the occurrence of corresponding multiple mutations in the parasite would be of lower value in a multifactorial system than in the monofactorial system hitherto used so widely in Europe.

SELECTION PRESSURES IN RACE FORMATION

It may be significant that physiologic races of nematodes have been found primarily in the genus Heterodera (21, 25, 26, 34, 35, 36, 51, 73, 74, 78, 79, 116, 132) and the genus Meloidogyne (31, 32, 49, 85, 88, 110, 119, 138, 148). The exceptions include evidence of physiologic races in Ditylenchus species (12, 76, 125) and in Radopholus similis (Cobb, 1893) Thorne, 1949, the burrowing nematode (33).

In both Meloidogyne species and Heterodera species the most critical selection pressure that provides the direction for genetic change has probably been enforced starvation. In Heterodera, because the host range in very narrow, the growing of resistant hosts has the effect of cutting off the food supply. Nematodes are obligate parasites (113); under conditions of such drastic environmental changes, populations will either become reduced in size to the point of extermination or the species will evolve in response to this change. Any surviving individuals must, of necessity, possess preadaptive morphological or physiological characters in the direction of the environmental change.

In Meloidogyne, the incidence of physiologic races has been noted primarily under conditions where their natural host range was forcibly restricted by greenhouse culture or by culture in restricted field plots. Thus, although Giles and Hutton (49) could demonstrate a breakdown in a resistant tomato variety under restricted plot culture in 5 years, they found no such breakdown in the same tomato variety when it was repeatedly grown under commercial field conditions with a susceptible tomato variety. Similar results were found by Allard with lima beans (3). The formation of physiologic races could therefore be the result of a restricted host range, either natural or artificial. A wide host range is apparently not conducive to race formation, because selection pressure exerted by starvation is weak or absent.

In theory it should be possible to prevent or retard race formation in nematodes by reducing the selection pressure in that direction. The results of Giles and Hutton with resistant tomatoes, and those of Allard with lima beans, indicate that when these two crops are grown in the field, physiologic races present no problem. Can the explanation be that, under field conditions, the nutritional needs of root-knot nematodes are met by other equally acceptable plants such as weeds? Likewise, with the golden nematode, would a rotation, alternating resistant with susceptible varieties, slow down the formation of resistance-breaking races? There is need for additional experimental evidence here, although limited experiments from the Netherlands, England, and elsewhere would indicate great promise that the answers will soon be forthcoming. In this country resistance-breaking races have been shown to compete successfully with the parental populations (148).

It is possible that some of our chemical control measures have actually removed natural selection pressures. Whitehead (145) has suggested that soil fumigation kills soil fauna indiscriminately. As a result, the slow-growing nematode predators are killed, and fast-growing parasitic nematodes survive to dominate (145).

GENETIC RESEARCH WITH NEMATODES

Despite the importance of genetic variability in nematodes, genetic studies of nematode populations are almost totally unknown today. In a careful search of the literature few instances of research in interspecific hybridization were found. Sperm cells of the sugarbeet nematode, Heterodera schachtii Schmidt 1871, were found in the oöcytes of the clover cyst nematode, Heterodera trifolii Goffart 1932 (94, 95, 96). Second-generation females produced four types of larvae: Small, normal, giant, and morphologically abnormal. It was suggested that these changed populations arose from either gene mutation or polyploidy.

Cytological studies in the family Heteroderidae have demonstrated the occurrence of both parthenogenesis and sexual reproduction in this group of nematodes (24, 111, 135, 136, 137). In addition, various degrees of ploidy were discovered (136).

Although the appearance of physiologic races in Heterodera rostochiensis was noted nearly

10 years ago, there is no evidence of how the resistance-breaking character, acquired by this nematode, is inherited. Hybrids between the original parental nematode line and the resistance-breaking lines must certainly have occurred in nature, but they have never been reported under controlled conditions. Such hybridization could markedly alter the rate of establishment of new races. Genetic studies of the nematode are as important as similar studies in the host plant.

Hybridization of nematodes for a different objective was proposed by Dunnett (35). He suggested culturing a mixture of the Duddington and Bogshall strains on a susceptible host to build up a highly pathogenic strain for use in evaluation and selection of potato-breeding lines with combined resistance to both races. However, an identical program proved to be ineffective in the control of late blight. In the late blight program, potato clones were repeatedly developed with genes for resistance matching corresponding genes for resistance breaking of the pathogen. Such clones based upon gene-for-gene interactions served only to increase the selection pressure, which in turn, usually within a year, resulted in the formation of a resistance-breaking race of the pathogen. The above program, suggested by Dunnett in breeding potatoes resistant to multiple races of the golden nematode, has the same basic weakness; it provides a system whereby the pathogen mutates faster than the plant breeder can evolve the matching resistance to the newly formed races. The development of potato clones based upon this kind of multiple allele system (in contrast to a multiple gene system) can conceivably result only in perpetuating the race problem, but never in solving it.

ASSOCIATION OF NEMATODES WITH OTHER PLANT DISEASES

Control of nematodes by genetic resistance in the host plant is closely related to genetic resistance to other soilborne parasitic organisms. Thus, nematodes are responsible both directly and indirectly for diseases in plants. In many cases, nematodes, in addition to their own parasitic action, provide avenues of infection for the entities that cause bacterial, fungal, and viral diseases. Jenkins and Coursen (77) found that nematodes cause a host response that lowers genetic resistance to other diseases. Likewise, the bacteria that cause Granville wilt of tobacco are not strong primary invaders and probably seldom infect tobacco in the absence of nematodes (83). Hence genetic resistance to nematodes would often enhance resistance to other disease-causing organisms. These relationships have been reviewed recently in detail (19, 70, 100, 104, 105). In some instances, nematodes caused no evident plant injury, but acted solely in providing avenues of infection (1, 86, 120).

On the other hand, soilborne pathogens may in turn directly affect nematode populations. Increased populations of the tobacco stunt nematode, Tylenchorhynchus claytoni Steiner 1937, and the meadow nematode, Pratylenchus penetrans (Cobb, 1917) Filipjev & Schuurmans Stekhoven 1941, were found surrounding roots of Alaska peas when Fusarium and Rhizoctonia were present in the soil, as compared to plots where the nematodes alone were present near the pea roots (29).

CONTROL OF NEMATODES BY RESISTANT VARIETIES

Nematode control through use of resistant crop varieties has occupied the time and efforts of many workers in the past 40 or 50 years, and there is a rich and plentiful source of information on this subject. For example, a list of plant varieties resistant to root-knot nematodes required nearly 90 printed pages in 1941 (139). Reviews of past and current work along these lines are available (89, 114). A partial summary of breeding research on some farm crops is shown in table 1.

Rohde (114) indicated that plants are resistant to nematodes for one or more of the following reasons:

(1) The plant is not attractive. The roots may lack an attractant or may produce a toxic substance.

(2) The host tissues are not suitable for continued nematode feeding. In hypersensitive reactions, the plant tissues die so rapidly that the nematode is isolated in necrotic tissue and its development is hindered.

(3) The host fails to respond to the presence of parasite. For example, galls or giant cells

Table 1.--Partial summary of research on crop evaluation and breeding for nematode resistance

Crop	Nematodes to which resistant	Citations to research workers	How resistance is inherited	Authority
Alfalfa	Root knot Stem nematode	58, 98, 107, 108, 124, 126, 128	Multigenic	58, 124
Beans (green and limas)	Root knot	3, 8, 9, 14, 75, 144	Two recessive genes.	8, 14
Barley	Cereal root	2, 25, 26	--	--
Clover	Root knot sp.	6, 10	--	--
Corn	Corn stunt	97	Recessive	97
Cowpeas	Root knot	9	Dominant	9
Cotton	Reniform	13	--	--
	Haplolaimus sp.	15	--	--
	Rotylenchus sp.	15	--	--
	Tylenchorhynchus sp	15	--	--
	Trichodorus sp.	15	--	--
	Root knot	87	--	--
Cucumbers	Root knot	41, 149	--	--
Fruit and nut rootstock	Root lesion	82	--	--
Muskmelons	Root knot	41	--	--
Oats	Cereal root	28	--	--
	Stem nematode	57	--	--
Onions	Stem nematode	11, 38	--	--
Lespedeza	Root knot	59	--	--
Peaches	....do	122, 123, 143	Dominant	143
Peppers	....do	60, 61, 62	--	--
Potatoes	Golden	21, 34, 71, 72	Single Dominant	72
Rice	Rice white tip nematodes	2 2	--	--
Sugarbeets	Sugarbeet	4	--	--
Safflower	Root knot	109	--	--
Soybeans	Soybean cyst nematode	116	-- --	-- --
Sweet potatoes	Root knot	22, 23, 40, 45, 46, 102, 142	Dominant	45
Tobacco	Root knot sp.	16, 20, 27, 52, 53, 54, 55, 66, 80, 90, 121	....do	20
	Pratylenchus sp.	53, 54, 55	--	
Tomatoes	Root knot	30, 39, 43, 47, 48, 64, 68, 84, 103, 115, 141	Single Dominant	7,147

may not form, or they may not form sufficiently for nematode reproduction.

(4) The plant responds physiologically, morphologically, or in other ways that react adversely on the parasite.

(5) Genetic (and other) reactions of the plant are modified by its environment. Such effects include temperature, mineral nutrition, soil textures, and age and vigor of plant.

Genetic resistance is thus an established method in the effective control of several nematodes. For example, the use of resistant potatoes reduced the population of golden nematodes by as much as 99 percent in 2 years (50). Likewise, the use of resistant rice varieties almost eradicated the seedborne nematodes, which cause white tip disease of rice (5).

A detailed review of the inheritance of plant resistance has been made by Hare (63).

Another aspect of breeding for nematode control that should not be overlooked is to search for tolerant hosts that will yield well in the presence of nematodes. Although these are less satisfactory than resistant hosts, because they help to maintain nematode populations, they are nevertheless useful for making a crop when other types of nematode control are not feasible.

NATURE OF NEMATODE RESISTANCE

The nature of some forms of nematode resistance has been studied in detail (32, 43, 54, 57, 67, 91, 112, 113, 114, 118, 129, 139, 146). This kind of research is the keystone to any sustained program of developing genetic resistance to nematodes. Some interesting developments in this field should be noted. Rohde (112) found the enzyme cholinesterase in all species of nematodes tested, and he attributed the nematocidal effect of an extract from asparagus to a cholinesterase inhibitor. Many of the recent organic phosphate chemicals so effective in controlling serious plant pests are likewise esterase inhibitors (17). A systemic organic phosphate has been found to eliminate nematodes from the tubers and roots of potato plants under greenhouse conditions (67).

Potato clones can be developed that have significant differences in cholinesterase inhibition of foliar extracts (99). Genetic resistance to potato leafhoppers and flea beetles has been positively correlated with a higher content of cholinesterase-inhibiting substance (69). It would be interesting to learn whether these same insect-resistant lines would also be resistant to nematodes for the same reason. The mechanisms involved in these observations need further study, especially since Steele and Price (129) reported no toxic effect of diffusates and extracts of asparagus roots on the sugarbeet nematode, Heterodera schachtii, in contrast to Rohde's results.

Mountain and Patrick (93) found that amygdalin from peach roots was hydrolyzed by nematode enzymes, releasing hydrocyanic acid, to the detriment of both host and parasite. The nematode enzyme, a beta-blucosidase, may enter into other host-parasite reactions. In plants there are many other naturally occurring glycosides that could be involved in similar breakdown and result in resistance to nematodes.

METHODS OF BREEDING NEMATODE-RESISTANT PLANTS

When nematode resistance is found within a particular crop species, no serious problems of breeding are encountered, unless the resistance character is closely linked to some other highly undesirable character, as in the case of tobacco (20). Transfer of resistance to acceptable crop varieties is largely through hybridization followed by selection in the segregating progenies. Mass selection is sometimes preferable to the backcross method in such programs (124). Thus, by intraspecific hybridization, the resistance in Nemagreen, a root knot-resistant lima bean, was developed from a lima bean grown by the Hopi Indians. Likewise, the root knot resistance of the sweet potato variety Nemagold came from types grown in New Jersey, the origin of which is obscure. Similarly, Catskill strawberry, Conch cowpea, Copper Gem onion, Auburn 56 cotton, Oakview Wonder Pepper, Menaguard peach, Delmar and Bragg soybeans, Nemastan and Lahontan alfalfa, and Bluebonnet 50 rice all came from resistant segregates within the original crop species. No doubt additional sources of intraspecific resistance can be found in almost any crop, with continued search and improved methods of testing. For example, plants both resistant and susceptible to the stem nematode are thought to occur in all commercial alfalfa varieties and can undoutedly be found by proper evaluation experiments (124).

However, the most valuable germ plasm for nematode resistance is found frequently in species quite distantly related. In such instances, special techniques must be used.

Thomason and Smith (134) and McFarlane et al. (84) were able to cross the root knot-resistant Lycopersicon peruvianum (L.) Mill. with the tomato by culturing the hybrid embryos on aseptic agar media. Attempts to cross these two species without using embryo culture techniques had previously failed, though it is interesting that Porte and Walker (103) subsequently made this same cross without resorting to embryo culture techniques. The resistance from L. peruvianum is somewhat unique because it involves similtaneous resistance to four species in the genus Meloidogyne, though a somewhat similar condition was found in Korean lespedeza (59). It is also interesting that the plants homozygous for the dominant allele have a resistance index approximately twice that of the heterozygous plants (7, 147).

A more complex technique was required to transfer the high level of resistance from Nicotiana repanda Willd to tobacco, N. tabacum L. N. repanda was found to be highly resistant to six species of root-knot nematodes (16). However, hybridization of N. repanda with both diploid and tetraploid forms of N. tabacum resulted in failures for Burk (unpublished), though sterile and abnormal hybrids and tobaccolike plants with no resistance were reported elsewhere (80, 121). Burk and Dropkin (16) suggested a bridging technique, whereby the resistance of N. repanda could first be transferred to N. sylvestris Speg. and Comes and from N. sylvestris to N. tabacum. This has resulted in tabacum-like plants, which are highly resistant or immune to the same six species of nematodes for which the original parental species showed resistance.

SUMMARY

In spite of the problem of physiologic races of nematodes, plant breeders have developed numerous varieties of plants with resistance to several species of nematodes. The net result has been the reduction in crop losses, caused by nematodes and other organisms, that may be associated with the disease complex. Germ plasm for resistance may usually be found within a crop species or transferred by several well-known plant breeding techniques from a related species to that crop species. We would suggest that the use of multigenic resistance, coupled with rotations of susceptible and resistant host and nonhost plants, can reduce or even prevent the tendency toward race formation. Despite the fact that breeding research to control nematodes started nearly 50 years ago, there are virtually limitless unexploited opportunities in the field of effective biological control of nematodes through the use of resistant crop plants.

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PLANT RESISTANCE AS A MEANS OF CONTROLLING INSECTS AND REDUCING THEIR DAMAGE[1]

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Among various general means of injurious insect control, using intentionally selected resistant host plants differs from the other insect-control methods in at least three respects. The differences have both facilitated and retarded extensive use of plant resistance as a means of insect control.

First, the entomologist attempting to develop insect-resistant plant varieties requires willing and enthusiastic assistance and cooperation of a plant breeder, who is cognizant of possibilities of this type of insect control and who will risk having his breeding plots damaged and results of his other experiments often badly distorted by insect infestation.

The Kansas Agricultural Experiment Station has released to Kansas farmers from 1926 to date about 14 varieties representing 5 species of crops, each more resistant to 1 of a total of 8 different insects than competing varieties grown previously. This has been largely the result of 39 years of cooperation between entomologists and agronomists.

Second, on the favorable side, the effect of a resistant variety is cumulative and persistent, whereas that of an insecticide is sudden and decreasing in effectiveness until and unless reapplied. Successful use of a resistant variety often removes the resisted insect so that farmers, county agents, and even entomologists and agronomists become unfamiliar with it. This is in contrast to insecticides, where the chemical must be applied from one to many times a year and then repeated in later years, often in heavier dosages against an increased insect population, or in different formulation for populations that develop resistance to the first formulation.

The continuous effect of control by use of a resistant variety contrasts with the sometimes cylic control attained by parasites and predators, where there are periods of alternate abundance of injurious insects and their predator and parasitic enemies. That does not mean that insecticides or parasites should not be used, but that resistant varieties give a different kind of control.

The third difference between resistant varieties and other control measures, especially long-standing resistant varieties, is their treatment in textbooks of applied entomology. Information in most cases ranges from at best somewhat less than enthusiastic comment to statements that indicate gross misinformation. Somewhat in defense of this situation is that textbooks cannot ordinarily be expected to be up to date even at time of publication, but ordinarily one expects information available in journals within the past 5 years to be in advanced textbooks. There have been some exceptions, such as the books by Wardel (1929) and Isely (1942).

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As an example of misinformation on varieties resistant to insects, the following is quoted from one of the most widely used texts and reference books on economic entomology by Metcalf, Flint, and Metcalf, "Destructive and Useful Insects," 4th edition, 1962, page 535: "Some varieties of wheat have been found resistant to Hessian fly, but up to the present time, no varieties have been found sufficiently resistant to attacks of this insect, and having other desirable qualities, to warrant recommending them generally in any of the large wheat growing areas."

Let us look at the facts. Four years before this book was published, six varieties of wheat had been listed (Painter, 1958) as having been recommended by 10 State experiment stations as resistant to the Hessian fly and also satisfactory in other respects. One, the variety Pawnee, became the leading wheat in acreage in 1949 in the United States--strong evidence of "having other desirable qualities." At the time, Pawnee was recommended and occupied nearly 6 million acres in Kansas alone and over 11 million acres in the United States (Clark and Bayles, 1951). Six million acres certainly qualify as a "large wheat growing area."

Another wheat variety, Big Club 43, from soon after its distribution and since, has occupied about 98 percent of the acreage in California formerly infested by the Hessian fly. It was so successful in virtually eliminating the Hessian fly in that area that no more research could be done, and the U.S. Department of Agriculture experiment station concerned with this insect in California was closed. This level of control of an insect has rarely been obtained by other methods.

In the 1961-62 wheat crop, Gallun (1962, 1965) reported that 17 wheat varieties resistant to the Hessian fly occupied up to 72 percent of the wheat acreage in 25 States. The varieties include five genetic sources of resistance, and then occupied a total of 4 1/2 million acres. This recent increase in Hessian fly-resistant wheat varieties reflects in particular the long-time studies at the Indiana Agricultural Experiment Station in cooperation with the U.S. Department of Agriculture, in addition to the research at the Kansas Agricultural Experiment Station. It also reflects recently expanded interest in noninsecticidal methods of insect control.

In contrast to the text book statement quoted, there now is no Hessian fly-infested major wheat growing area where at least one adapted Hessian fly-resistant wheat variety cannot be grown. There is now no need of loss because of the Hessian fly. Control can be achieved without extra cost except perhaps for new seed, which may also give other benefits. This can be said of no other method of control for a widespread insect.

No information on well-documented and successful instances of insect control by host plant resistance is given in any general textbook of applied entomology. Examples are readily available. The classical example of control of the grape phylloxera by such means (Howard, 1930) should be as well known to students of entomology as control of the cottony-cushion scale by the vedalia lady beetle. But it is not. With such misleading or lack of information in textbooks, an appreciation and knowledge of plant resistance as a method of insect control cannot be expected of many entomology graduates.

I now wish to comment on procedures and principles involved in developing host plant resistance and on the present status of some research projects dealing with the subject.

Plants that are inherently less damaged or less infested than others under comparable environments in the field may be called resistant.

The first step in any resistance program is to find genetic factors for resistance. The chance of finding resistance is more or less proportional to the number and diversity of the plants and varieties of a crop species that can be studied, and to the control of the infesting population of insects used during the period of search. The best insect population to be used for infestation is not always the highest possible population of insects, but rather the level of population that gives the maximum difference between resistant and susceptible plants. Thus far, genetic factors for resistance have been found wherever adequate search has been made.

For example, in a search for Hessian fly resistance, tests on about 3,000 foreign and domestic wheat varieties were reported at one time (Jones, 1945), with about 6 percent considered to be resistant. Over the years, two or three times that many have been studied. Six genes have been recorded for Hessian fly resistance in wheat and several more are known to exist.

For the recently introduced cereal leaf beetle, Oulema melanopa (L.), a total of over 30,000 wheat, oats, and barley varieties have been exposed to infestation the first year. About 12 percent of the 16,095 wheat, 4 percent of the 5,423 oats, and less than 1 percent of the 8,634 barley varieties were considered resistant (unpublished). Since the basis of resistance is frequently complex, it is important to find as many different genetic factors as possible for all components of resistance to the same insect. Often this can be done by employing different measures of resistance: Egg counts, estimates of damage, effect of plant on the insect, and others.

"Currently, a cooperative project, being sponsored jointly by the International Maize and Wheat Center of the Rockefeller Foundation in Mexico, the Instituto Nacional de Investigaciones Agrícolas of the Government of Mexico, and Kansas State University, is concerned with a search for insect resistance in races of corn from the corn germ plasm banks of Latin America. These germ plasm banks consist of over 18,000 samples of corn still being grown near out-of-the-way villages throughout Latin America. This seed is kept viable by cold storage and periodic replanting. The visible range of characters of grain, cob, plant, and maturity is far greater than the range of such characters in available Corn Belt or other inbreds and hybrids. Some races are believed to carry various genes from Tripsacum. Both situations suggest strongly that these corns should carry genes for insect resistance not now available in corn grown in the United States.

In less than a year's study, evidence that this is true is beginning to be found. Replicated nurseries of 80 samples of these races were planted in several places in Kansas and once each month at Tepalcingo, Mor., Mexico. Clear differences were evident between races in damage by the fall armyworm, Spodoptera frugiperda (J. E. Smith); stalk borers, Zeadiatraea spp.; the cornleaf aphid, Rhopalosiphum maidis (Fitch); and especially thrips, Frankliniella occidentalis (Perg.). Additional research will be needed to confirm the results and much more to incorporate the genes in useful inbreds or new synthetic varieties. The study so far is only a small beginning, but it illustrates the importance of examining many and diverse plants in the search for resistance.

The next step in a resistance study is to obtain evidence that the supposed resistance is an inherited character. This requires testing of progeny of the plants selected as being resistant, and also studying such plants and their progeny under various environmental conditions.

If the resistant plants are selections from a satisfactory adapted cultivar, they may be combined or selected to produce an acceptable variety for immediate agronomic testing, increase, and distribution. If, on the other hand, the new resistant plants are not adapted in any important way, they must be crossed as needed with plants of satisfactory varieties and reselected in succeeding generations. Both the original and later selection processes must be designed (1) to test the maximum number of plants with the minimum labor and time and (2) to test for as many genetic factors or components of resistance (Painter, 1951, p. 25) as possible with the same or succeeding procedures.

Resistance as seen in the field or greenhouse is made up of one or any combination of these components--nonpreference, antibiosis, tolerance. In the field especially it is usually impossible to tell which components are involved in any example of resistance or the proportion of each present. It is most important to incorporate into any proposed resistant variety as many genes as possible for two or more components of resistance, since such provisions make much more difficult the natural selection of biotypes able to infest or injure or both the resistant variety. Identifying the component or components early in any case of resistance is important in designing testing procedures. Detailed analyses of the physical or biochemical bases of these components have been of practical value on only two occasions so far. It cannot be overemphasized that a detailed knowledge of cause is not needed in the practical use of insect resistance. There have been occasions, however, when a futile search for cause has delayed such use. On the other hand, resistant versus susceptible plants have not had sufficient use on the study of insect feeding behavior and physiology. Resistance must be found in each case before it can be studied.

Much has been learned in recent years of the food relations of insects to plants and especially of differences between plant species in the relationships (Beck, 1965). But there remains only one example, that of resistance factor A (6-methoxybenzooxazolinone) and its biochemical precursor (RFC) in corn, in which a biochemical difference between varieties of a crop plant has been experimentally and satisfactorily associated with resistance to an insect, the European corn borer, Ostrinia nubilalis (Hübner), (Beck, 1960).

A knowledge of the several bases of resistance will eventually be of value in other ways besides contributing to the understanding of resistance. Identification of chemical or physical factors concerned in preference, nonpreference, or repellence may lead to other uses in control of insects through the identified chemicals or related synthesized ones that improve on nature. Likewise the identification of bases of antibiosis could lead to new and presently unknown kinds of insecticides, less toxic to mammals and perhaps highly specific to certain insects. The search for causes of tolerance may lead to ways of improving the ability of plants to withstand related insects, perhaps through manipulation of plant hormones, enzymes, or similar substances. The use of a knowledge of bases of resistance in the search for resistance through chemical tests of plants instead of using insects is unlikely to be practical for several reasons. An exception may be with such plants as trees. With insects such as the spotted alfalfa aphid, for example, thousands of plants can be screened in a few weeks, the susceptible plants killed by the insect, and only presumed resistant ones left. Few chemical tests would permit such "screening" so quickly or so cheaply and still leave only the few resistant plants. Furthermore, using insects permits one to find other resistance factors with other bases that would be missed by chemical tests. Such additional findings, as indicated above, would be of major importance.

In contrast to lack of value in a search for resistance, the availability of chemical or physical tests associated with specific genes for resistance could speed up the combining of two genes for resistance in a single variety when the two can otherwise be identified only genetically.

The search for biochemical substances associated with the finding of host plants by insects is highly important in insect biology, and information obtained should find increasing value in insect control and survey. But such a study must not be confused with a search for the bases of resistance.

The value of a few examples of resistance emphasizes some principles concerned with using resistant varieties for insect control.

The spotted alfalfa aphid, Therioaphis maculata (Buckton), was first observed in the United States early in 1954 damaging alfalfa in the Southwestern States, reaching Kansas late the same year. By 1956, it had spread into 30 States. Susceptible alfalfa plants of any age or size were rapidly killed. Cooperative studies between agronomists and entomologists of the Kansas Agricultural Experiment Station, the Fort Hays Branch Experiment Station, and the U.S. Department of Agriculture were begun in 1955 in a "crash" program to supply farmers with an adapted, spotted aphid-resistant alfalfa variety (Harvey et al., 1960).

It was quickly evident that a few individual plants resistant to this insect occurred in alfalfa varieties. Using a great number of plants, the resistant ones were selected from the adapted variety Buffalo in a series of entomological tests, and the 22 best plants were selected on the basis also of agronomic tests. The plant progeny from those 22 clones constituted the variety Cody. In the greenhouses (fig. 1) under aphid attack, the difference between Cody and Buffalo, from which it was selected, is clearly evident (fig. 1). The same has been true in the field, where Cody was compared with other varieties. The young alfalfa plants in August and September were especially susceptible to aphid attack, yet in fields where plants of susceptible varieties were severely injured or destroyed, Cody survived with little loss of stand. The original records, on which the decision to release Cody was made in 1959 (table 1), show that its resistance is due to the two components, tolerance and antibiosis. Nonpreference may also be involved, but information on that point is not yet clear.

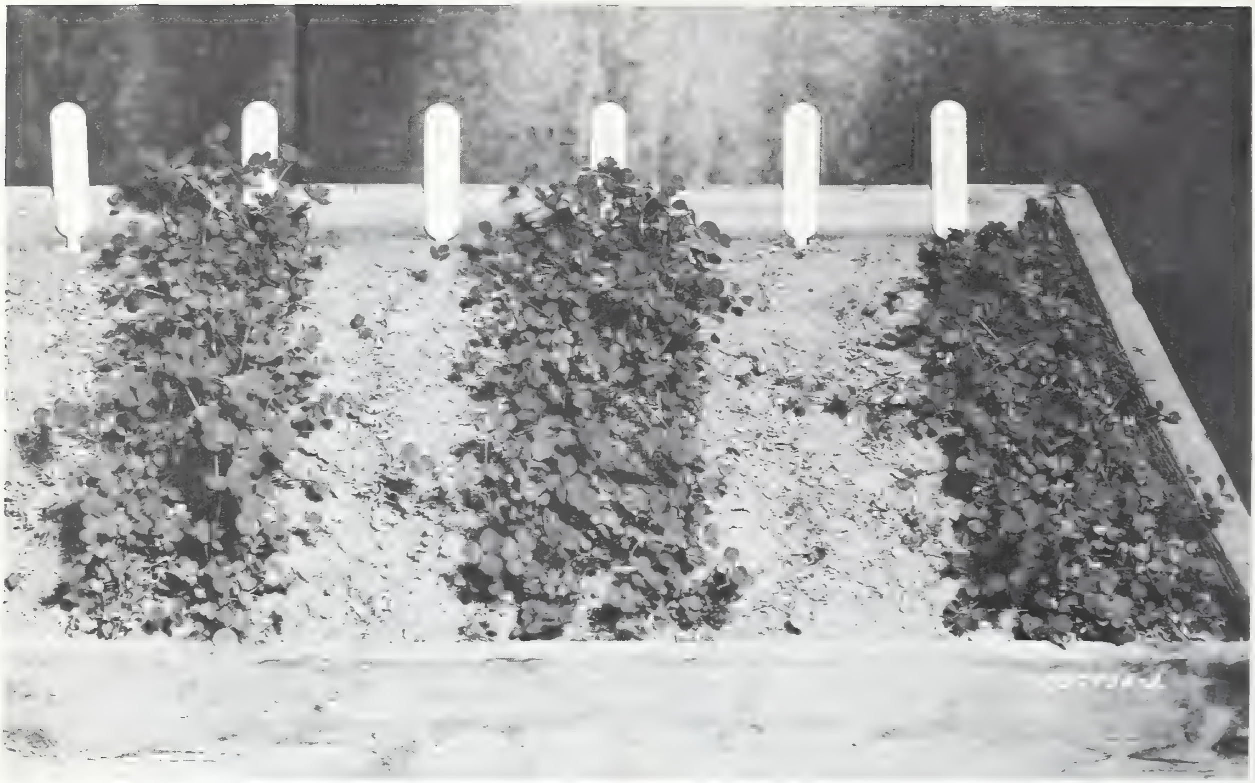


Figure 1.--Seedling survival in greenhouse of Cody (labeled 22 clones) compared with Buffalo alfalfa after infestation with spotted alfalfa aphids. (Harvey et al., 1960.)

Table 1.--Original records at time of release of Cody. (Modified from table 1, Harvey et al., 1960.)

Alfalfa variety	Nymphs per female in 7-8 days		Mean seedling survival (3 tests)
	Live	Dead	
	Number	Number	Percent
Resistant cody			
Clones or seedlings...........	0.05	1.04	73
Lahontan clones or seedlings...	.3	.9	66
Susceptible Buffalo clones or seedlings................	5.29	1.08	7

For a number of years, Oklahoma and, to a less extent, Kansas have carried on research toward production of small grains resistant to the greenbug, Schizaphis graminum (Rondani). That aphid comes into Kansas from the south, and often severely damaged barely, wheat, and oats in late fall and early spring. A single genetic factor for resistance is known in wheat and two in barley. Wheat and barley hybrids that carry the genes for resistance have been studied in yield tests in both States. Resistance to greenbugs (fig. 2) can be just as striking as resistance to the spotted aphid in alfalfa in either the green house or the field. The components of resistance involved are different from those in alfalfa to spotted alfalfa aphid. In both wheat and barley the principal characteristic of the resistant plants has been their ability to withstand infestation (tolerance). In wheat, fewer young are usually produced on resistant

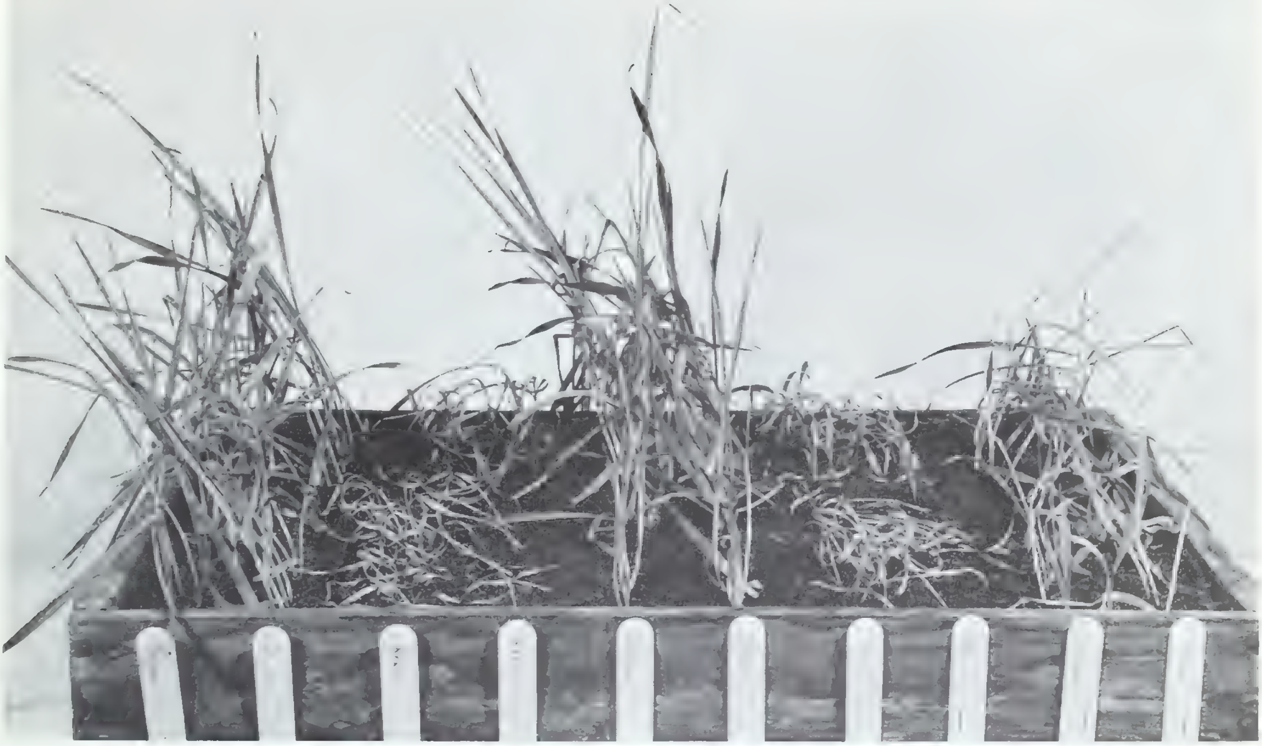


Figure 2.--Relative damage by greenbugs to seedlings of Reno and Dicktoo (standing) barley grown in greenhouse. Similar differences occur in field.

plants, but often the differences are not statistically significant. In barley, aphids on resistant plants usually produce about half as many young as on susceptible plants (table 2).

The barley variety Will, a selection from a cross Kearney (resistant) Rogers (susceptible), produced at the Oklahoma Agricultural Experiment Station in cooperation with the U.S. Department of Agriculture, has been released to farmers in Oklahoma and in 1964 approved for release to farmers in Kansas. We anticipate that when the variety Will is planted on large acreages, a 50 percent reduction in greenbugs each generation as they move across Oklahoma and Kansas in the spring should furnish considerable protection to susceptible wheat, barley, and oats and reduce the aphid population migrating north. Thus, it is important to emphasize that equivalent or similar resistance in the field or greenhouse can result from different components for resistance and different amounts of each in a variety. Cody alfalfa and Will barley are excellent examples

Table 2.--Greenbug resistance in Will barley compared with resistant and susceptible variety in Oklahoma tests

Variety	Greenbugs per foot	Average plants per foot	Bushels per acre
	Number	Number	Number
Infested:			
Omugi.....	31	17	70.6
Will......	24	16	68.6
Rogers....	53	3	9.8
Not infested:			
Omugi.....	0	17	65.2
Will......	0	17	69.2
Rogers....	0	21	72.5

of different components being alike as judged by final results.

Value of Resistance: The resistance of wheat varieties to the Hessian fly is a long-time illustration of the value of such varieties.

In Kansas from 1871, when it reached the eastern counties, until the late 1930's and 1940's, when resistant varieties provided the needed control, the Hessian fly caused yearly losses from $5 million to $25 million in outbreak years. Kawvale, approved in 1932 in Kansas, was the first Hessian fly-resistant wheat variety released by an experiment station and recommended for growing by farmers in a State. It reached a maximum of over one-half million acres in Kansas about 1939 (Clark and Quisenberry, 1948) (table 3). Pawnee was released to Kansas farmers in 1943 because it was superior to Kawvale in several agronomic and milling quality characters. By 1951, it had reached its maximum acreage in Kansas of nearly 7 million acres, including more than 90 percent of the wheat acreage in 27 counties. Principal acreage was in the eastern half of Kansas, where the Hessian fly had been commonly injurious. For this area also the highly fly-resistant variety Ponca was approved for farmer use in 1951, and reached a maximum Kansas acreage of 1,787,500 in 1959. Meanwhile, the resistant varieties had a disastrous effect on the Hessian fly population in the eastern half of Kansas, despite all counties still having some susceptible varieties (fig. 3). Furthermore, the leading resistant variety, Pawnee, carried at best only about 50 percent resistance. A new Hessian fly-resistant variety, Ottawa, was released in 1960 and reached a Kansas acreage of about 800,000 by 1964. It is still increasing in acreage.

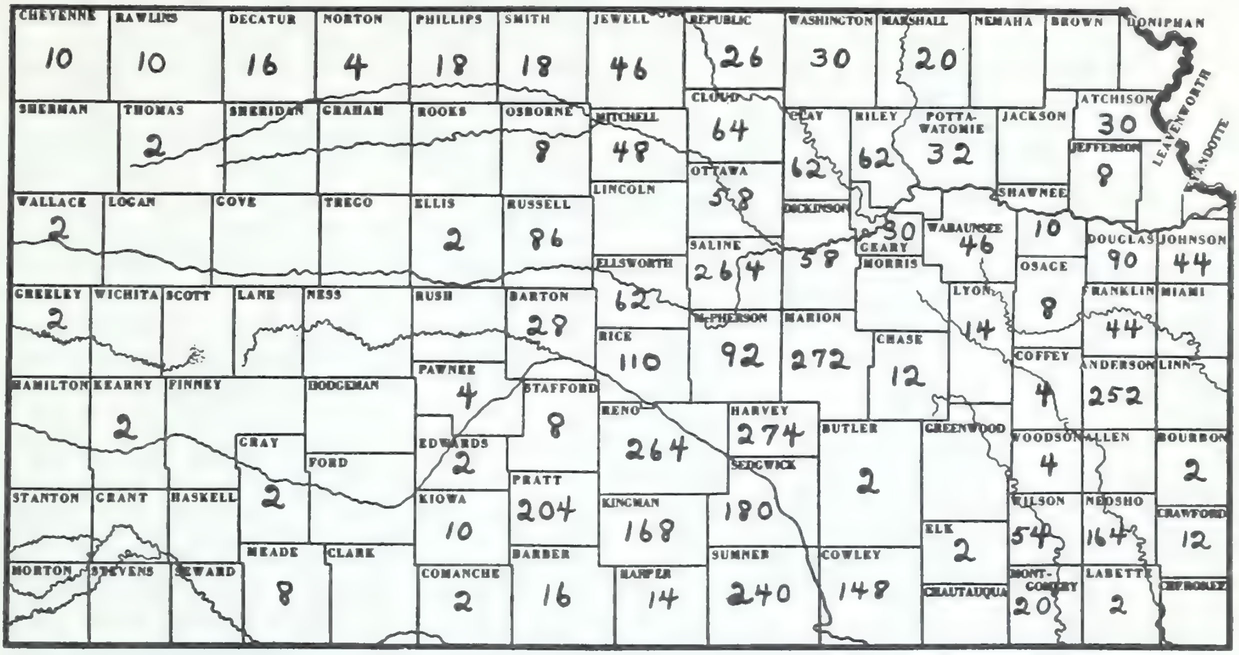
Meanwhile, in 1958 a severe outbreak of wheat streak mosiac occurred in north-central Kansas. All Hessian fly-resistant wheat varieties are susceptible to that mosaic, but some Hessian fly-susceptible wheats carry some tolerance to the disease. Those varieties increased in acreage at the expense of Hessian fly-resistant ones. There has not been time enough between the first widespread outbreak of wheat streak mosaic in 1950 and 1958 to find tolerance to it and combine the tolerance with fly resistance. Hybrids with both characters are now in yield nurseries. The effect on the fly population of the decreasing acreage of resistant varieties was quickly evident (table 4).

The Fort Hays Branch Experiment Station was in the area of heavy infestation and afforded new evidence of the effectiveness of the resistant varieties. It also afforded an opportunity to compare the variety Turkey, which was commonly grown in Kansas when work begain on Hessian fly resistance in 1914, with recently fly-resistant varieties (fig. 4). A return to the use of more resistant varieties over the area in 1963 and 1964 was accompanied by a short drought that further reduced the fly population. A review of the history (table 4) of the use of these resistant wheat varieties shows that it has been necessary to replace older resistant varieties with new ones as new varieties improved, for other characters become available.

The Hessian fly has always been considered highly destructive (Hyslop, 1938; Brown, 1964). It ranked ninth among the 49 individual insects for which estimates of damage were made by Hyslop. In Kansas from 1923 to 1927, the estimated average annual loss was 18,500,000 bushels, or 15 percent of the crop; and from 1926 to 1935, the estimated annual loss was 5,731,000 bushels worth $4,033,000 (depression dollars) (Hyslop, 1938). During 1947-60 in

Table 3.--History of Kansas Hessian fly-resistant wheat varieties. From Kansas (State Bd. Agr. Div. Statistics reports)

Variety	Year distributed	Kansas maximum acreage and year	Remarks
Kawvale............	1932	500,000 (1939)	Now replaced by Pawnee.
Pawnee.............	1943	6,663,830 (1951)	Kawvale resistance.
Ponca..............	1951	1,787,533 (1959)	Marquillo and Kawvale resistance.
Ottawa.............	1960	872,562 (1964)	Ill. No. 1 resistance.



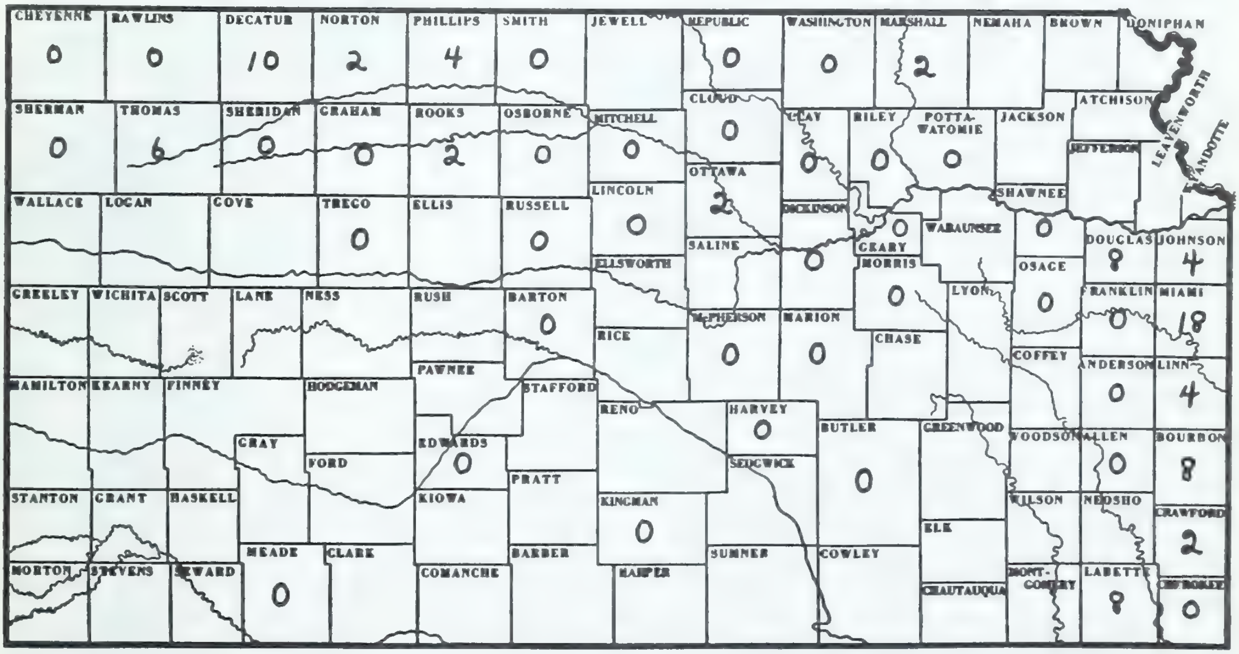


Figure 3.--Comparison of Hessian fly infestations in Kansas: Top, 1945; bottom, 1957. Maximum number of puparia per 100 stems. (From cooperative U.S. Dept. Agr. and State survey.)

Table 4.--Acreage of Hessian fly infestation and Hessian fly-resistant varieties in north-central Kansas

Year	Hessian fly[1] infestation	Resistant varieties per county[2]	Remarks
	Percent	Average percent acres	
1957........	1.1	56.5	--
1958........	1.1	56.8	Mosaic outbreak.
1959........	3.6	53.1	--
1960........	2.2	21.3	--
1961........	8.1	25.6	Hessian fly increase.
1962........	13.5	15.4	Hessian fly outbreak.
1963........	8.4	34.2	--
1964........	.6	44.6	Decrease in Hessian fly aided by drought.

[1] From cooperative insect report.

[2] From Kansas State Bd. Agr. Div. Statistics reports.

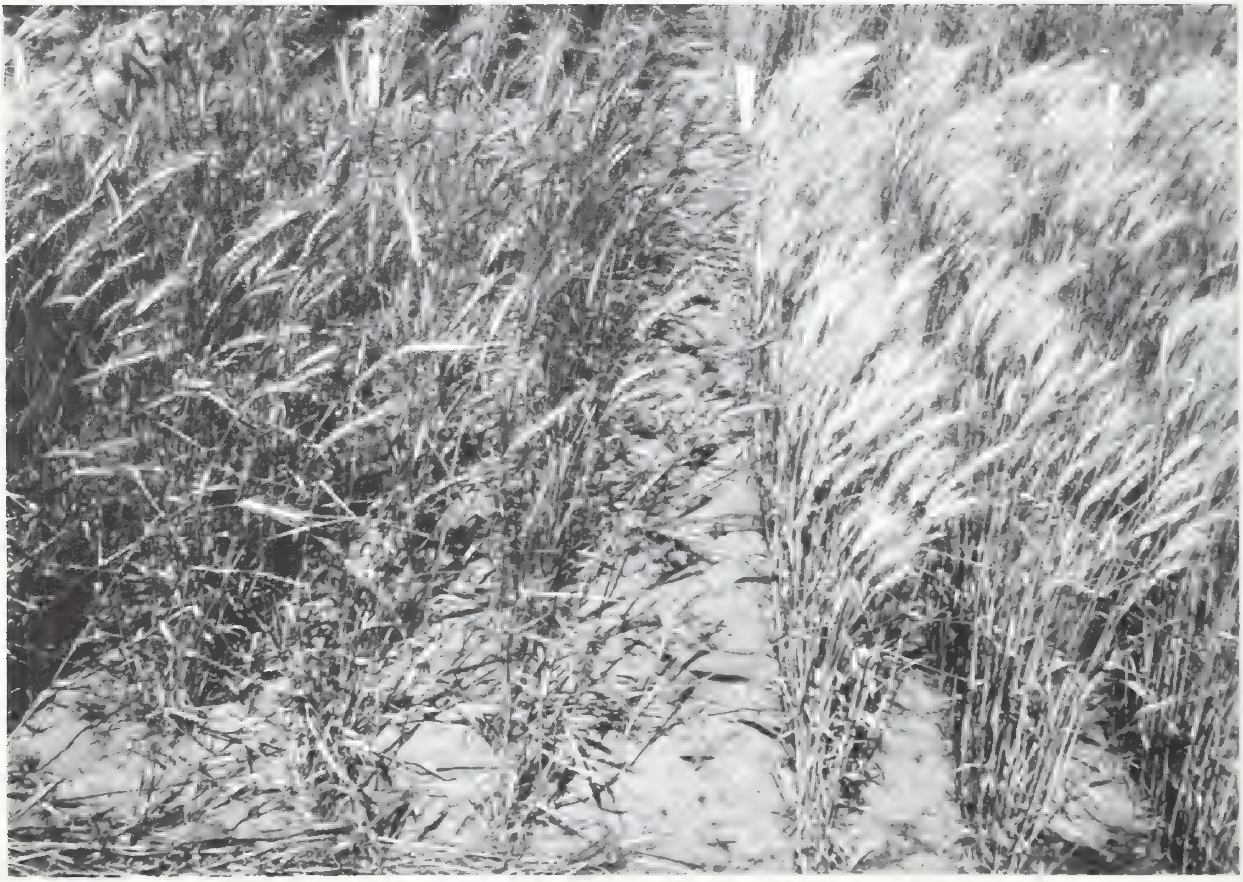


Figure 4.--Comparison of selection of Turkey (left) with Hessian fly-resistant hybrid (right) after infestation by insect. (Photographed June 15, 1962, Hays, Kans.)

Kansas, many acres were planted with Hessian fly-resistant varieties in the eastern two-thirds of the State, where the insect previously had been abundant. Surveys each year showed only an occasional wheatfield with a low Hessian fly infestation. Over much of the State the insect was absent or nearly so (fig. 3). Hence a conservative estimate of saving from planting Hessian fly-resistant wheats in Kansas would be 5 million bushels per year. During the earlier part of the period the wheat was needed to help feed war-torn Europe.

SUMMARY

A consideration of plant resistance as a means of controlling insects and reducing their damage suggests several characteristics and principles concerned with such practical use of resistant varieties.

(1) Successful use of host plant resistance requires team research by at least an entomologist and a plant breeder.

(2) The effect of a resistant variety is ordinarily cumulative and persistent in its effect on the insect population in contrast to insecticides, which are sudden and decreasing in effectiveness unless reapplied. Where resistant varieties are effective, farmers and others tend to forget about the insect controlled and why, until they change to a susceptible variety and learn again.

(3) Most young entomologists have little or no knowledge of the use of resistant varieties, primarily because of misinformation or lack of information in many currently used applied entomology textbooks--a situation that should be corrected.

(4) The first step in any resistance program is to find inherited factors for resistance. The chance of finding such resistance is largely proportional to the number and diversity of plants and varieties studied. Thus far, genetic resistance has been found wherever adequate search has been made. Some examples include resistance to the Hessian fly, the cereal leaf beetle, and resistance of corn to insects.

(5) Evidence of the inheritance of resistance factors and of the components of resistance involved are necessary early in the studies of resistance. It is best to make full biological analyses before proceeding with chemical or physical analyses. Detailed research on bases of resistance have so far been of little value in practical use of insect resistance. Since such information is of high theoretical interest, eventually patterns of importance in practical ways of insect control should emerge.

(6) The same high levels of resistance to insects in two plant varieties may be reached by different components of resistance or different levels of effects of the same components. For example, Cody alfalfa carries a high level of tolerance to the spotted alfalfa aphid and also an ability to suppress aphid reproduction almost completely in comparison with susceptible varieties.

Will winter barley suppresses greenbug reproduction by only about 50 percent, but has a very high level of tolerance to the insect. Yet field or greenhouse experiments show about the same levels of resistance in Cody alfalfa to the spotted alfalfa aphid and Will barley to greenbugs in comparisons with susceptible varieties of the same crops under heavy attack by the two aphid species.

(7) During 32 years, the Kansas Agricultural Experiment Station has produced and recommended four Hessian fly-resistant wheat varieties for farmers. They have been grown where adapted in Kansas in "Large wheat growing areas" from 1/2 million to 6 2/3 million acres at time of maximum planting of each.

A continuing change in plant disease conditions, milling and baking requirements, and availability of varieties improved in other respects has resulted in replacement of earlier fly-resistant varieties by others superior in such resistance or in other characteristics and appears to be the likely pattern in many cases of insect resistance.

(8) The Hessian fly-resistant wheat varieties available in the United States and adapted to and recommended in a variety of areas should afford low-cost control of the Hessian fly to individual farmers in any important wheat-growing area where fly infestation normally has occurred.

(9) Research on breeding crop varieties resistant to the more important insect pests and some minor ones should always be a continuing part of any plant breeding-insect control program.

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THE FUTURE OF ANIMAL BREEDING FOR RESISTANCE TO DISEASE AND PESTS

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Estimates of the annual losses of cattle, sheep, swine, poultry, and their products in the United States from infectious and noninfectious diseases amount to $1.52 billion. Losses from parasites add another $330 million, totaling $1.85 billion. This is equivalent to about 11 percent of the income from livestock and livestock products. The cost of drugs and treatments makes the figures even more staggering. Suffice it to say that one of the major means of lowering the cost of livestock production is through reduction of the toll taken by diseases and pests. Although U.S. losses per farm unit are high, livestock producers here fare better than those in many other areas of the world. This evident when we consider that the United States has an annual extraction rate for livestock to 30 percent or better, as compared with 5-15 percent in many of the developing countries.

Considering that genetic variation in response to disease, including environmental stress, has been observed in all cases adequately studied, it is a temptation to believe that breeding for disease resistance should be a prime objective for the animal breeder at this time. The temptation becomes even greater when we consider the emphasis and success of the plant breeder in disease control.

Even though many of the basic laws of inheritance apply equally to plant and animal life, breeding programs vary because of peculiarities and restrictions imposed by each species considered. These differences include mode of reproduction, reproduction rate, value of individual, length of reproductive life, and

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[1] The authors acknowledge the help of L. B. Crittenden, H. L. Marks, G. M. Sidwell, and H. O. Hetzer in assembling data and materials.

generation interval. Furthermore, except for poultry, each commercial producer must in varying degrees conduct his own breeding program. With these factors in mind, we will consider what possibilities are open to the animal breeder for disease, abnormalities, and pest control.

QUALITATIVE TRAITS

A wide variety of congenital abnormalities that interfere with body function have been reported for all classes of livestock. Stormont (1961) described over 90 abnormalities for cattle, sheep, swine, horses, and poultry. Those of genetic origin are amenable to control if the "carriers" can be detected. Detection of carriers is straightforward in the case of the dominant anomalies, such as achondroplasia in cattle and lethal gray in sheep. Most congenital disorders, for which some proof of inheritance is established are, however, due to a single autosomal recessive gene with no visible effects on the heterozygous individual. Some of the more common lethals or semilethals in the homozygous state are muscle contracture, semihairlessness, and leglessness in swine, mulefoot, dwarfism, and shortspine cattle.

What percent of our breeding program should be directed toward the detection and elimination of these recessive genes? Consider the case of dwarfism in beef cattle. Limited evidence indicates that the heterozygote has a slight selective advantage because of its compact conformation, but since the homozygous recessive is completely rejected, the frequency of the gene is held in check.

If all the herd sires carried the dwarf gene and nothing was done except to eliminate the easily detected dwarf, the incidence would stabilize at about 14.6 percent of all calves born. If only 80 percent of the sires used were carriers, the incidence would be 10 percent; 50 percent carrier sires, 4.4 percent; 40 percent carrier sires, 3 percent; and 20 percent carrier sires, less than 1 percent dwarfs (Emmerson and Hazel 1956, Smith 1959). If control efforts are confined to pedigree selection on immediate ancestors, the incidence will remain rather low. Losses from dwarfism and other autosomal recessives cause only a small portion of losses as compared to other diseases, and since they cannot be eliminated completely, efforts of balance must be such that the return is greater than the expense of the control program.

INHERITED SUSCEPTIBILITY

In addition to the clear-cut anomalies, susceptibility to such diseases as cancer eye, bloat, and milk fever appear to be genetically affected. Hereford cattle are most prone to afflictions of the eye, but the condition is usually not a problem except in the latitudes of high solar radiation intensity. French (1959) observed that eye cancer is unusual in animals less than 4 years of age, and susceptibility reaches a peak at about 7 to 8 years. Bonsma (1949) reported that the presence of a ring of pigmentation around the eye gave almost complete protection. Since lid pigmentation is rather heritable (0.6-0.8), those breeders plagued by this condition may be advised to pay some attention to eye pigmentation in their breeding program.

Although genetic susceptibility to such diseases as bloat and milk fever has been demonstrated, more information is required before breeding recommendations can be made.

QUANTITATIVE TRAITS

Diseases caused by pathogens result in the greatest economic losses, but the genetic picture is complicated by genetic variation in the pathogens, the genetic environmental interaction of the animal, possible acquired immunity, and perhaps yet unrecognized factors. In spite of these obstacles, there is some evidence to support selective breeding for reduction or control of pathogenic diseases. The example presented here are some of those for which present evidence holds limited promise.

Mastitis

Mastitis is the most complex and costly disease afflicting dairy cattle (about $400 million annually) in the United States. In the past 30 years, several reports have been published on clinical cases, family histories, and some quantitative studies that indicate a partial hereditary basis. Lush (1950) analyzed data from 27 New Zealand herds, classifying cows as resistant, no mastitis up to 8 years, and susceptible, or those having mastitis. Using this all or none classification, about 85 percent of the daughters of susceptible dams were susceptible, whereas only 55 percent of the daughters of resistant cows were susceptible. Intraherd regression of daughter on dam yielded a heritability of 0.38 ± 0.32. Legates and Grinnells (1952) reported a heritability of 0.27 ± 0.10, using data from 11 herds and classifications of streptococci or staphylococci with a leucocyte count of one-half million or more cells per milliliter in any quarter during any sampling period.

A study by Young et al. (1960) is the most comprehensive to date. Their definitions of mastitis were (1) clinical - the percentage of months in lactation during which the cow had mastitis; (2) bacterial infection - scores of monthly milk samples; and (3) leucocyte score - computed by summing the logarithms of the monthly leucocyte counts. The estimates of heritability and repeatability are given in table 1.

All these studies may be criticized for employing inadequate definitions of mastitis susceptibility. Since the scores utilized do not indicate sampling from a normal distribution, estimated progress in selection is not a very suitable criterion for use in a breeding program. Even so, the estimates are in close agreement and show important differences between animals.

If we accept these heritability estimates and assume that resistance to mastitis is at least as heritable as milk production, what emphasis should be given in a breeding program? Even though several, including Hutt (1958) and Fredeen (1963), have advocated direct selection against susceptibility, little seems to have been done. The causes might be as follows:

(1) To date we do not understand enough about the disease to construct a good index for ranking animals. For example, in the study of Young et al. (1960), the genetic correlation between clinical mastitis and bacterial infection of 0.23 to 0.29 indicates that selection on either of these would have little effect on the other. The genetic correlation between leucocyte count and each of the other indicators of mastitis of 0.80 or higher would indicate this may be an effective criterion. However, since leucocytes are one of the most important defense mechanisms of the body, we may be selecting the most susceptible instead of the most resistant cows as parents.

The work of Schalm et al. (1964) illustrates the point, as they found that mastitis developed in all quarters of cattle secreting cell-free milk when challenged with approximately 8,000 *Aerobacter aerogenes*, but partial protection was afforded when the fore milk contained 200,000-350,000 leucocytes per milliliter. Recent studies at Beltsville, Md., have shown a wide range (<30,000 to 10>million) of leucocytes shed by normal noninfected quarters (Smith and Shultze, 1964), whereas the number shed by infected quarters ranged from <30,000 to > 50 million. Leucocyte counts also appear to be affected by the type of bacteria infecting the quarter.

(2) If selection is to be effective, it must be measured rather early in the reproductive life of an individual. The measure employed by Lush required cows to reach 8 years before they were considered resistant. Legates and

Table 1.--Heritability and repeatability estimates for clinical mastitis, bacterial infection, and leucocyte count

Method of evaluation	Heritability		Repeatability
	Daughter-dam regression	Paternal sister correlation	Intracow correlation
Clinical mastitis.................	0.06 ± 0.18	0.79 ± 0.21	0.31 ± 0.06
Bacterial infection...............	.18 ± .14	.87 ± .21	.24 ± .06
Leucocyte count...................	.38 ± .20	.23 ± .22	.42 ± .05

Grinnells eliminated first calf heifers from their analyses because they had a high resistance as compared with other cows.

(3) Before deciding to include mastitis resistance in a selection program, we must know how it relates to other economic traits. For example, some have stressed the importance of the teat sphincter as a barrier to udder infections. McEwan and Cooper (1947) found a higher frequency of mastitis among fast milking cows than among slow milking cows. They suggested breeding for slow milking cows as a possible means of controlling mastitis. These findings have been verified by Dodd and Neave (1951), but they point out that differences in milking rate cannot account for the large differences between herds in frequency of mastitis.

By contract, present emphasis on selection for high production and culling cows for economic reasons gives some weight to mastitis resistance. O'Donovan et al. (1960) reported a depression of 10 percent in the lactation milk yield of infected cows. Other reports indicate depressions ranging from 5 to 24 percent, depending somewhat on the definition of mastitis used. If it is safe to assume a relationship between susceptibility and severity of mastitis, there is automatic selection against mastitis susceptibility when we choose those individuals that actually produce the most milk.

A study of DHIA records by Asdell (1951) reveals that about 22 percent of the cows on test are removed from herds each year. Almost half of these are culled because of low production and udder trouble. The fact that 2.5 percent (about 40,000 cows) of the population is culled annually because of udder trouble indicates a rather strong rejection of mastitis-susceptible cows.

(4) Since most of the possible genetic progress would come through selection and proving of sires, a uniform national program of scoring and officially recording a large segment of the cow population would be required.

Thus, until research provides a better understanding of the disease and its relation to other economically inherited traits, we have no basis for advocating drastic changes in our concept of breeding better dairy cattle than through selection for production.

Other Diseases

The problems of breeding for the control of mastitis have been discussed at length because similar situations presently exist with most pathogenic diseases in farm livestock. For example, (1) in swine--atrophic rhinitis (Koch et al., 1958; Schulz, 1962), brucellosis (Cameron et al., 1943), and pig dysentery (Englehart, 1949); (2) in sheep--Escherichia coli infection (Fredeen, 1963), scrapie (Dickinson and Young, 1964; Draper and Parry, 1962; Pattison, 1964), and fleece rot (Dunlop and Hayman, 1958); (3) in poultry--avian leucosis (Siegmund, 1961), Rous sarcoma virus (Waters and Burmester, 1961; Crittenden et al. 1965), Salmonella pullorum (Hutt, 1949), fowl typhoid (Lambert and Knox, 1932), and poultry coccidosis (Champion, 1954; and (4) other pathogenic conditions too numerous for discussion at this time.

It should be pointed out that although scrapie has been included as a pathogenic condition, there are two schools of thought on its origin--one as a genetic abnormality supported by Draper and Parry and the other pathogenic postulated by Dickinson and Young.

There are other diseases caused by pathogenic organisms, which take heavy tolls in livestock productive performance, but for which there is little evidence of genetic resistance. Such a disease is hog cholera. Still others, such as foot and mouth disease, have supporters as being more prevalent among European-type cattle than zebu stock, but such observations have been largely on newly introduced animals. Comparisons between zebu stock and cattle from European countries, where the disease has been prevalent for a long time, will be needed for an adequate test.

RESISTANCE TO PARASITES AND PESTS

The term "parasite," as used here, applies to forms of animal life that have been adapted to live on or in farm livestock, and "pest" refers to those insects that prey on livestock.

Protozoa Diseases

Some examples of protozoa diseases for which genetic immunity has been claimed are tick fever (Kozyelka, 1929; Riek, 1962), heartwater (Bonsma, 1949), African trypanosomiasis, anaplasmosis, piraplasmosis, leptospirosis, and East Coast fever in cattle. Most of these observations are based on a comparison of zebu and European breeds and could be due to differences in the degree of infection rather than genetic immunity. The greater resistance of the zebu may be because the vector has difficulty penetrating the skin.

Wilkinson (1962) suggests some evidence in Illawarra Shorthorn heifers in tick resistance, which was attributed to differences in hair follicle depth. Observations by McDowell et al. (1964) for an 8-year period, however, showed no significant differences among Red Sindhi (a zebu breed from India), Red Sindhi-European crosses, Brahma, Angus, Brangus, Holsteins, Jerseys, and European crosses in resistance to anaplasmosis where horse flies and mosquitoes were the major vectors. Mahadevan (1964) reported a heritability for East Coast fever of near zero.

Based on present evidence, it appears that the animal breeder should continue to rely on induced immunity and vector control programs until a better understanding is obtained of the feasibility of selecting for modification of skin and hair coat traits as natural repellents.

Internal Parasites

What little is known about disease resistance in sheep is largely concerned with internal parasitism; however, at present, there is no clear evidence that selection can be effective in developing resistant strains. Stewart et al. (1937) showed that breeds differ in resistance to continuous exposure to Ostertagia circumcinta, with the Romney being most resistant, followed by the Rambouillet, Southdown, Shorpshire, and Hampshire, with some variation between individuals. Gregory et al. (1940) also noted variation between individuals of the Romney breed for this same parasite. Emik (1949) suggests evidence of genetic differences between lambs in resistance to trichostrongylid infection and calculated a heritability of 0.22 ± 0.41. Warwick et al. (1949) showed that selection of survivors after an intensive exposure to Haemonchus contortus caused a significant increase in survival rate over a 9-year period. There are similar bits of evidence for these and additional parasites in other classes of livestock.

Thus, meager evidence suggests selection could be effective, but, as with mastitis, the measures employed so far are to subjective to warrant consideration by animal breeders. Furthermore, assuming the same rate of genetic mutation in a host and parasite, the fecundity of the parasite is much greater; therefore, the genetic changes in the host will be relatively unimportant. Since young animals are most susceptible, systems of feeding and management and methods of induced immunity appear as the most fruitful areas of research.

Pests

Observations made in this field, such as those by Bonsma (1949), Veiga (1964), Kozyelka (1929), and others, point to the lesser attack of zebu cattle by ticks. Among the reasons advanced are the shorter hair coat, greater number of hair follicles per unit of area, thicker skin, denser epithelial layer, greater depth of hair follicle, and perhaps peculiar secretions from the sebaceous gland exudated through the skin, which acts as repellents. These observations have not as yet been sufficiently proven as contributors against susceptibility for the animal breeder to utilize them in the identification of resistant individuals. Nevertheless, more specific experimentation should prove fruitful, particularly in view of the increasing concern over pesticide residues in human and animal health and the fact that insects rapidly develop resistance to pesticides (Johnston et al., 1954).

OTHER TRAITS

Heat Resistance

Over the past two decades, much has been written on the resistance of some groups of animals versus others for heat resistance, such as Leghorn chickens, Merino sheep, and zebu cattle. Based on this evidence, those writing on breeding for disease resistance (Hutt, 1958; Fredeen, 1963; Shrode and Lush, 1947; and others) have advocated exploitation of indigenous stocks to increase resistance to environmental stress and thereby perhaps greater resistance to disease and pests.

In accepting this approach, we should recognize a high negative correlation between metabolic heat production and physiological tolerance--often used synonymously with heat tolerance. But there is a high positive relationship between the level of body temperature, metabolic heat production, and milk yield or growth rate. Hence, we have two conditions--one of physiological tolerance and the other of productive tolerance. If there is a negative relationship between physiological tolerance and productive performance, then certainly some minimum for productivity would be required before attempts are made to select for low body temperature. Perhaps the same phenomena could be applied to selection for disease resistance. In some environments it may have an inverse relationship to the direction animal breeders wish to go on productivity. Present evidence suggests attention to nutrition, management, and disease control is more worthwhile than selection for resistance to environmental stress until there is a clearer understanding of the physiological mechanisms involved in adaptability.

Sterility

Losses from reproductive failure constitute the greater loss among females in farm livestock. There is little evidence of genetic factors as a major cause, but Casida (1961) suggests that antibody production could be a possible factor. Thus, some cause of sterility may be indirectly related to disease conditions and should be considered along with attention to disease problems.

Hormones and Drugs

Increased use of drugs and hormones may solve, add, or create a whole host of new problems in disease control. There is already some evidence in the work of Landauer (1957) which has shown that treatment with insulin will produce the defect "rumplessness" in chickens.

SUMMARY

The foregoing discussion does not pose a very bright future for the animal breeder in controlling disease through genetics. Disease and parasite problems can be controlled largely by slaughter, vaccination, and a high level of sanitation. These solutions may not always be practical or feasible. The animal breeder must, therefore, ask himself how far he should go in eliminating diseases. Present genetically caused abnormalities can be controlled by recognizing the mode of inheritance and employing systematic breeding programs.

The recognized offenders of abnormalities that occur under certain environmental conditions can be eliminated; therefore, such conditions can be kept under fairly good control.

In the case of pathogenic diseases, most animals have a general resistance to one or more pathogenic organisms, but until research provides (1) a better understanding of the disease and its relation to other economic traits, (2) more precise means of classifying animals as to resistance, and (3) satisfactory identification methods that can be used early in life, selection for resistance is not warranted. A system of selection for these diseases would also be expensive, and there is no assurance that changes in organisms would not be greater or more rapid than genetic progress can be made in farm livestock. It appears that animal breeder should work closely with veterinarians and others in developing systems of sanitation and induced immunity to supplement the emphasis already applied through selection for maximum performance.

The era of breeding animals suited to existing natural climatic conditions seems passing; therefore, attention must be given to ways and means of controlling the environment in such a way as to make it optimum for maximum productive efficiency. If this trend is accepted, then techniques of management will probably be among the most fruitful approaches to lowering the costs of farm livestock losses caused by disease and pests. Resolving the best methods for this will require the teamwork of engineers, physiologists, nutritionists, and others.

The genetics of disease resistance should and must be continually pursued, but in this field the key to the future will be through studies of mechanisms rather than further search for the existence of genetic variability. This will involve a basic understanding of defense mechanisms inherent in the animal or those that can be supplemented or created later in life.

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PEST CONTROL BY PHYSICAL MEANS

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Physical methods of insect control bring instantly to mind such devices as the flyswatter or flypaper. But, in this case, a more sophisticated approach to this problem is intended. Here, the word "physical" refers to the luring of, the entrapment of, and the disposition of the insect pest by mechanical means.

The method of luring these insects is of primary importance, since the success or failure of the device is determined by the number of insects enticed into the device. Attractants of all types have been used. All have one characteristic in common, that of catching insects by capitalizing on their natural inborn senses. Historically, insect traps designed on this basis were used as early as the mid-1800's. True, these traps were simple devices, but they took advantage of specific insect habits. For instance, since the codling moth spins its cocoon in protected places on trees, Joseph Burrelle in 1864 suggested winding something around the trunks of apple trees or placing a cloth in the crotch and then destroying the trapped codling moth larvae by disposing of the cloth and winding material. Such traps and their modern successors have proven themselves useful tools in today's research as measurement devices. Recent studies indicate that insect traps, employing sources of electromagnetic energy as the attractant, may be used as effective devices for control, as well as measurement, of certain night-flying insects.

The following papers present an excellent cross section of present research in the use of insect traps for insect control: P. C. Callahan presents information, data, and theories in his paper, "Electromagnetic Communication in Insects," concluding that various species of moths may have communication devices that depend on the detection of energy in the far-infrared region of the electromagnetic spectrum. He indicates that such sensitivities might be used to advantage in control devices. S. O. Nelson and J. L. Seubert provide an excellent resumé of past and present research and its possible direction in the future in "Electromagnetic Energy and Sound for Use in Control of Certain Pests." F. R. Lawson, C. R. Gentry, and J. M. Stanley present the encouraging results of their tests involving the control of the tobacco hornworm with light traps in their paper, "Experiments on the Control of Insect Populations With Light Traps." To complete the picture, W. M. Carleton and R. D. Brazee point out the part the agricultural engineer can take in the studies on physical control of insects in the "Role of Agricultural Engineers in Pest Control."

ELECTROMAGNETIC COMMUNICATION IN INSECTS--ELEMENTS OF THE TERRESTRIAL INFRARED ENVIRONMENT, INCLUDING GENERATION, TRANSMISSION, AND DETECTION BY MOTHS[1]

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Jean Henri Fabre, the great 19th century French entomologist, in his classic work on the great peacock moth, established that certain species of moths could locate their mates over great distances. He hypothesized that either scent or hertzian waves were responsible for location and attraction of night-flying moths. Experiments I performed at the U.S. Department of Agriculture, Southern Grain Insects Research Laboratory, Tifton, Ga., indicated that for certain species of noctuids and sphingids location and attraction are accomplished by infrared electromagnetic radiation and that scent is responsible for species identification. Thus, in a sense, Fabre was correct in his hypothesis with regard to both scent and electromagnetic waves.

Sir William Herschel, in 1800, discovered the invisible electromagnetic energy of wavelengths beyond the red part of the spectrum. We now know that all objects whose temperatures are above absolute zero emit infrared (IR) radiation. Over the years, the gap in our knowledge of the spectrum between IR radiation and microwave radio frequencies has been slowly narrowed. Glagolewa-Arkadiewa (1924) demonstrated IR radiation of about 90 μ by exciting small hertzian oscillations in the form of brass filings in oil. Nichols and Tear (1923), using a diffraction grating for the measurements, demonstrated hertzian (far infrared) waves of wavelengths down to 220μ.

The standard for IR definition is the backbody, essentially any object that absorbs all received radiation. The intensity and wavelength of IR radiation depend on the absolute temperature in degrees Kelvin (°K.) of the emitting object and on its surface finish. The radiation and absorbing efficiency of an object are called its emissivity (ϵ) factor (table 1) and is unity (1) for a blackbody. A mirror is a poor radiator and absorber of IR, having an emissivity factor near zero. A black rough surface, such as lamp black, is extremely efficient as a radiator and absorber and approaches unity. Objects with an ϵ of less than unity are termed gray bodies. Most objects, including the moth and the human body, fall into this category.

Table 1.--IR emissivities (ϵ) for different objects at ambient temperatures (after Barnes 1963)

Material	Emissivity
Human skin	.99
Water	.98
Green plants	.95-.97
Lamp black	.95
Concrete, glass	.94
Paper, plastic	.92
Plastics	.88
Stainless steel, iron	.70
Plowed field, gravel	.28-.44
Polished cast iron, lead	.21-.28
Chrome	.08
Mirror	.02

IR radiation is often wrongly termed heat radiation, because it generates heat in any absorbing object in its path. However, light rays, X-rays, and even high-intensity radar beams have the same property. Since the IR band falls between visible light and radio (7.5×10^{-4} mm. to 1 mm., or in terms of microns 0.75 μ to $10^3 \mu$, it is extremely intriguing and demonstrates many of the characteristics of both. It may be focused by lenses and yet can be transmitted like radar or radio through materials that block visible light. As

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[1] After this paper was presented at Montreal, the author received a critical review from Dr. E. Okress of the Institute of Electrical and Electronics Engineers. Some of his comments are so pertinent that parts are quoted in this paper.

I have often stated in postulating my theories about the IR environment of night-flying moths, we are dealing with a region where light acts like radio and radio like light. Emphasis is added to my comparison by the use that present-day infrared technologists make not only of optics--refraction and reflection techniques--but also of radio techniques--waveguide and resonant cavities--to detect such radiation.

IR radiation has definite characteristics that make it useful for detection purposes (Hackforth 1960). IR systems, lighter, smaller, and less complex than conventional radar systems, do not generate the detrimental side lobes of radar. One great advantage of an IR system is that it is passive and requires no transmitter to obtain the return signal. In other words, it senses the object directly. These advantages are pointed out for the obvious reason that when location is concerned, the efficiency is indisputable whether or not such a detection system were to be utilized by man to detect rockets or is a facet of nature itself in the marvelous intricacies of insect life.

There is no doubt that moths are attracted to electromagnetic radiation. We are all familiar with the moths' propensity for the ordinary 60-watt incandescent lamp. Figure 1 gives the energy curve for such a transmitter. It is my contention that we have as much right to insist that the moth is attracted by the much greater energy of the longer wave IR output (a) as we have to insist that it is attracted by the lesser energy of the shorter wavelengths in the small visible area of the luminosity curve (b).

It is well known that the higher temperatures produce shorter wavelengths (light) and that λ max. displaces toward the longer and longer wavelengths as power and heat are reduced (fig. 2). This displacement becomes obvious when we hook a 60-watt tungsten lamp to a rheostat and reduce power. The visible spectrum shifts from white to red heat and finally to black heat as the filament "goes out," no

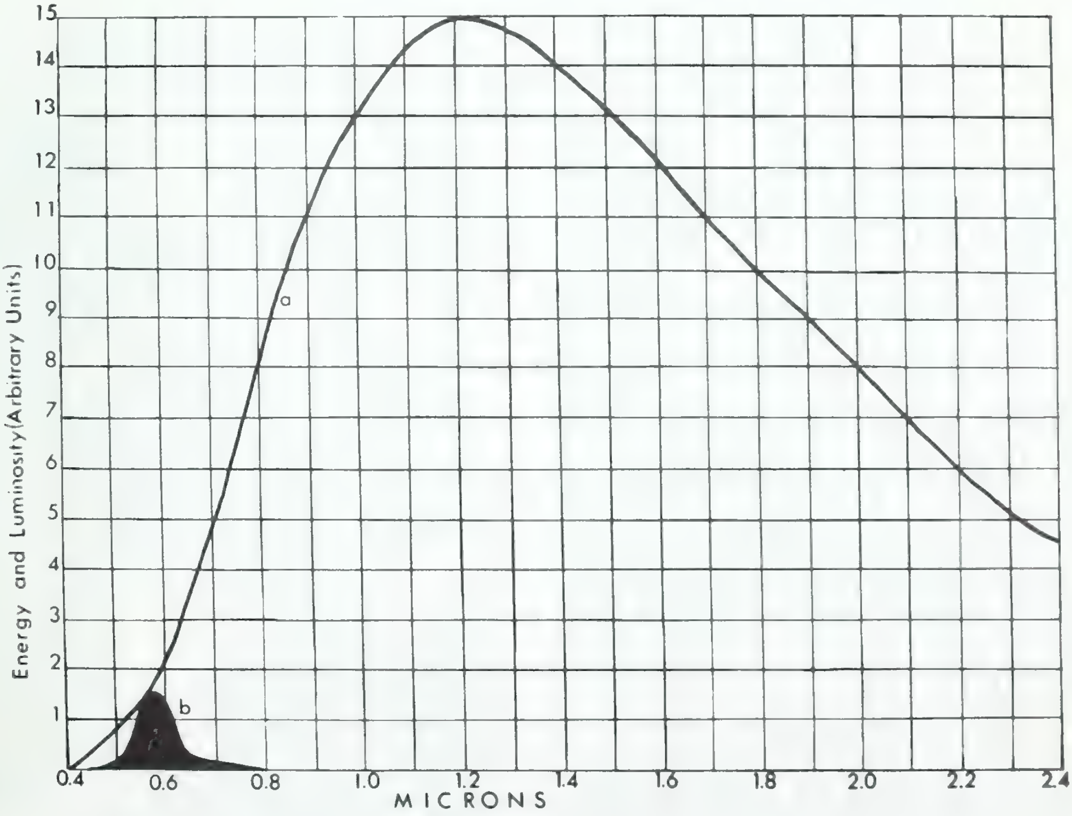

Figure 1.--Spectral energy curve (a) and luminosity curve (b) of tungsten filament at 2200 °K. (after Schilling 1940).

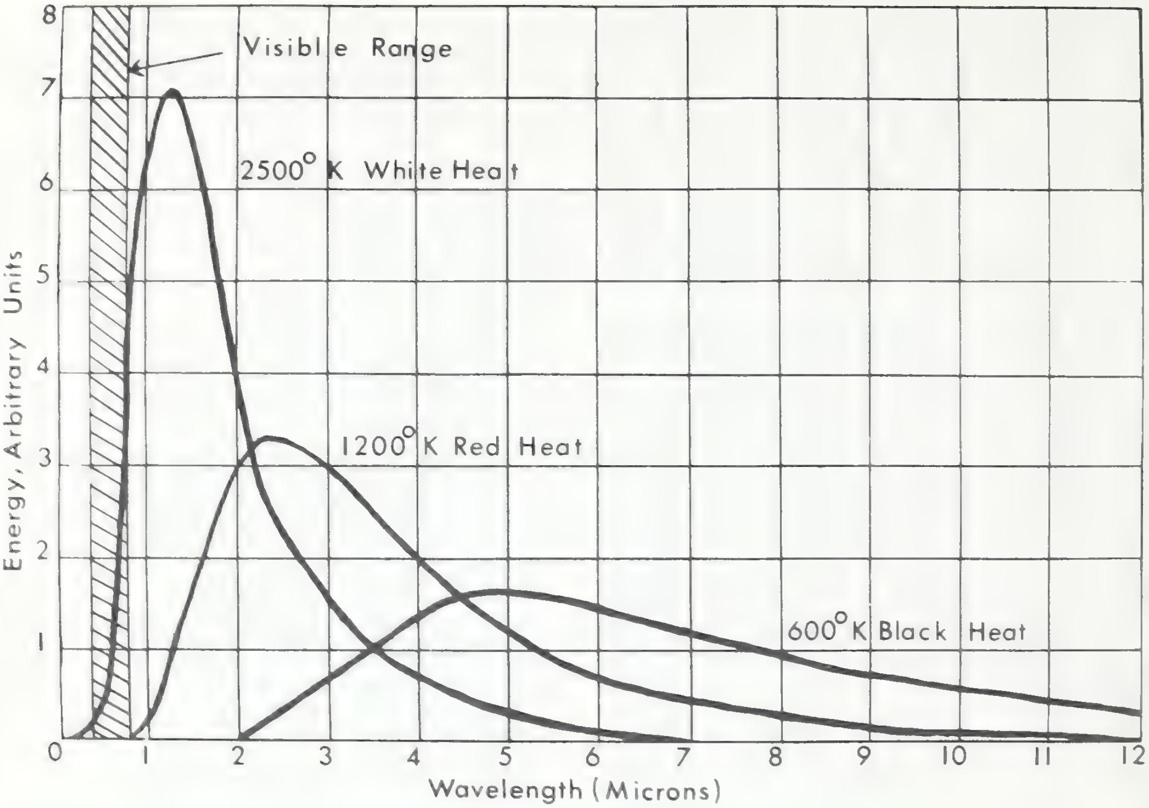

Figure 2.--Increase in mean wavelength of radiation as temperature is reduced (after Summer 1962).

longer sensitizing our eye (fig. 2). Inability of our eye to detect black heat does not mean that such a self-emitting body is not incandescent.

As Barnes (1963) pointed out, such objects emit no visible light and thus must be illuminated by some external hotter source to be detected by the eye. However, to any instrument having IR detection capabilities, these objects would be highly incandescent. All objects in nature, regardless of their temperature, are IR incandescent. Animals and plants are constantly absorbing and emitting IR radiation. In short, nature is inherently a thermal IR environment, and all objects in nature with high emissivity (table 1) are incandescent point sources of IR radiation.

BIOLOGICAL DETECTORS

If we are to assume that insects, and in particular moths, can detect IR, then we must examine closely their anatomy to determine whether they have any organs that might be considered as having an IR detector configuration.

The most obvious areas of interest for study are the compound eyes and the ocelli, both of which have optical configurations. Modern microwave techniques, however, indicate that the antennae also display certain characteristics that should be subjected to considerable investigation. Smith et al. (1957) noted that by using microwave techniques we may now observe heat radiations. Blackbodies in the form of lossy waveguide terminations are used to calibrate receivers in the 8-mm. wave band. We shall examine the antennae first.

Most moth antennae are very stable in free flight (Callahan 1965a), and are located forward and away from the body of the flying moths. Thus, the antennae sensilla, displayed against the nighttime background, are relatively free of any interference from the thermal emission of the moth's body.

In the microwave region of radio there are three tuneable frequency configurations called resonant cavities, which are classified according to their physical construction. They are the coaxial resonator, the waveguide cavity, and the rhumbatron or doughnut-shaped cavity. They take the shape of cylinders, rectangular prisms, or spheres. Rectangular waveguides are commonly used as resonant cavity devices in microwave radar. The cylindrical hollow waveguide and cylindrical coaxial resonator are the two configurations most nearly resembling the structural form of the antennal sensilla.

The present state of antennal morphology indicates that although some sensory sensilla may be hollow, others have processes originating at the sensory nerve cell that are channeled through a cuticular sheath and end in pores at the spine cuticle (Schneider 1964). If we consider these two types electrically, the former may resonate as hollow waveguides and the latter as coaxial resonators. Either type might also be filled with a liquid or other substance and thus be similar to a solid or liquid-filled dielectric resonator.

Okress (1965) stated, "In the case of solid or liquid dielectric waveguides, the electromagnetic energy exists in both solid or liquid dielectric and the surrounding air. For high real dielectric constants and for frequencies well above the cut-off valve, the energy is essentially confined in the solid or liquid dielectric. Since the cut-off wavelength depends upon the dielectric constant, no simple expression as previously given for the metallic case is possible.

"For single lobed directional radiators the asymmetric hybrid HE_{11} mode in dielectric waveguide has similar field configuration to that of the dominant (H_{11}) mode in hollow circular metal waveguide, except that the former (HE_{11}) has no cut-off (i.e., propagates at all frequencies). However, there is cut-off behavior with respect to all, including the H_{01} and E_{01}, other modes.

"In the case of the hollow dielectric cylinder waveguide, modes arise corresponding to those of the solid dielectric rod, but characterized by greater cut-off frequencies. However, in the case of the HE_{11} mode, no cut-off frequency exists again. Furthermore, hollow dielectric cylindrical waveguide can support a single mode (i.e., the fundamental HE_{11} mode). This is especially important for use as an antenna. This is done by reducing the ratio of wall thickness to real dielectric constant to a sufficiently small value. Furthermore, for thin wall dielectric waveguide essentially single-lobed radiation pattern may be realized. This follows for the HE_{11} mode when the wall thickness is small enough to make the hollow dielectric waveguide beyond cut-off for all other modes.

"It is for these reasons important to determine whether the insect's antennae are filled with high or low or no real dielectric constant liquid (e.g., water). It is also important to determine the real and complex dielectric constants of the dielectric antennae tubes and liquids, if any, contained therein."

Generally speaking, if we allow the inner conductor in a coaxial line to decrease in size, we can eventually remove it, and the magnetic field will be self-supporting. This then becomes the H_{01} mode in a circular waveguide (fig. 3). The resonant modes, which correspond to the lowest possible generated electromagnetic frequency, are labeled E_0 and H_0 modes. They are the lowest of an infinite number of frequencies at which a cavity will resonate. The cutoff wavelength of all modes in a circular waveguide is $\lambda \underline{c} = \frac{2 \pi a}{\underline{S}}$. The cutoff wavelength for the H_{01} mode in a circular waveguide is $\lambda \underline{c} = 1.6.40 \underline{a}$.

E- waves (fig. 4) are produced by calculating modes in rectangular waveguides and allowing the configuration to change from rectangular to circular. Where the configuration is changed, it may be necessary to have circular waveguides of different sizes for different modes if we are considering the same wavelength energy. The different sizes would be necessary, because the cutoff wavelength changes and the circular waveguide must be able to propagate the energy of the wavelength in the rectangular waveguide (Mariner 1961). Such is, of course, exactly what we have in the moth antennae. There are many different antennal sensilla and certain of them are of variable lengths in graduated steps (Callahan 1965b).

E- modes have an electric field parallel to the axis of the cavity (Young 1960). The E_{01} mode has a field that is constant with an angle a half wavelength in width along the diameter and a full wavelength along the axis. The E_{01} mode of the cylindrical cavity has a resonant

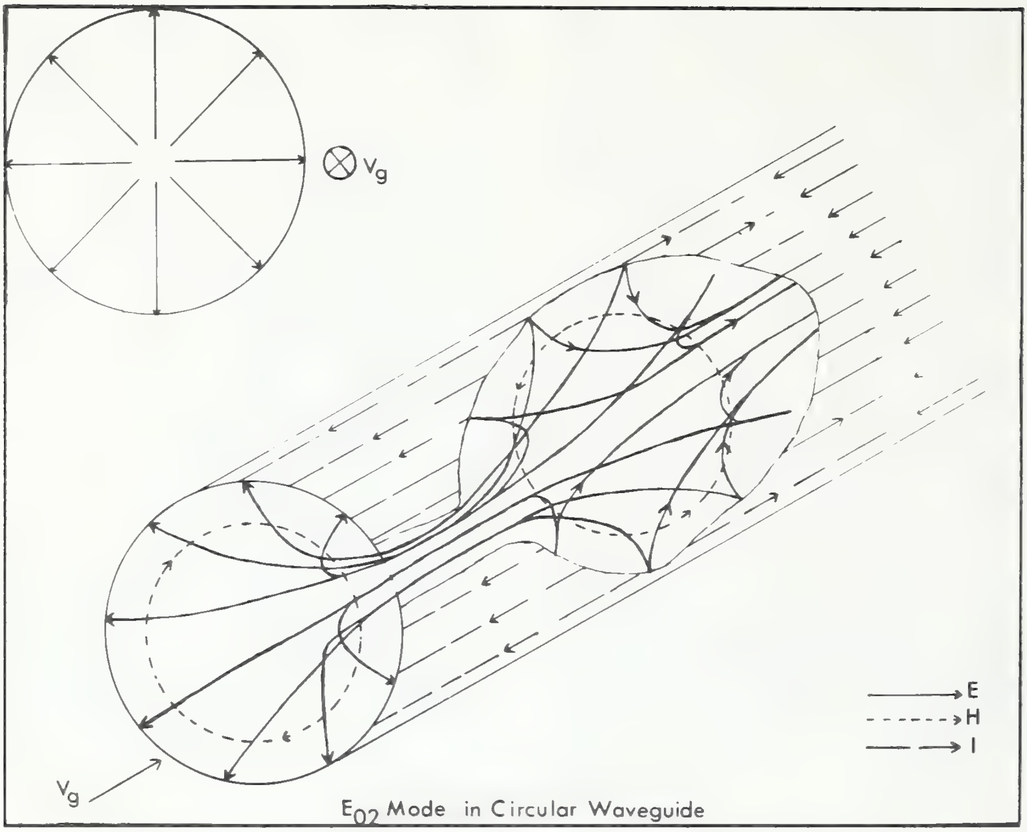

Figure 3. --H_{01} mode in hollow circular waveguide (after Mariner 1961).

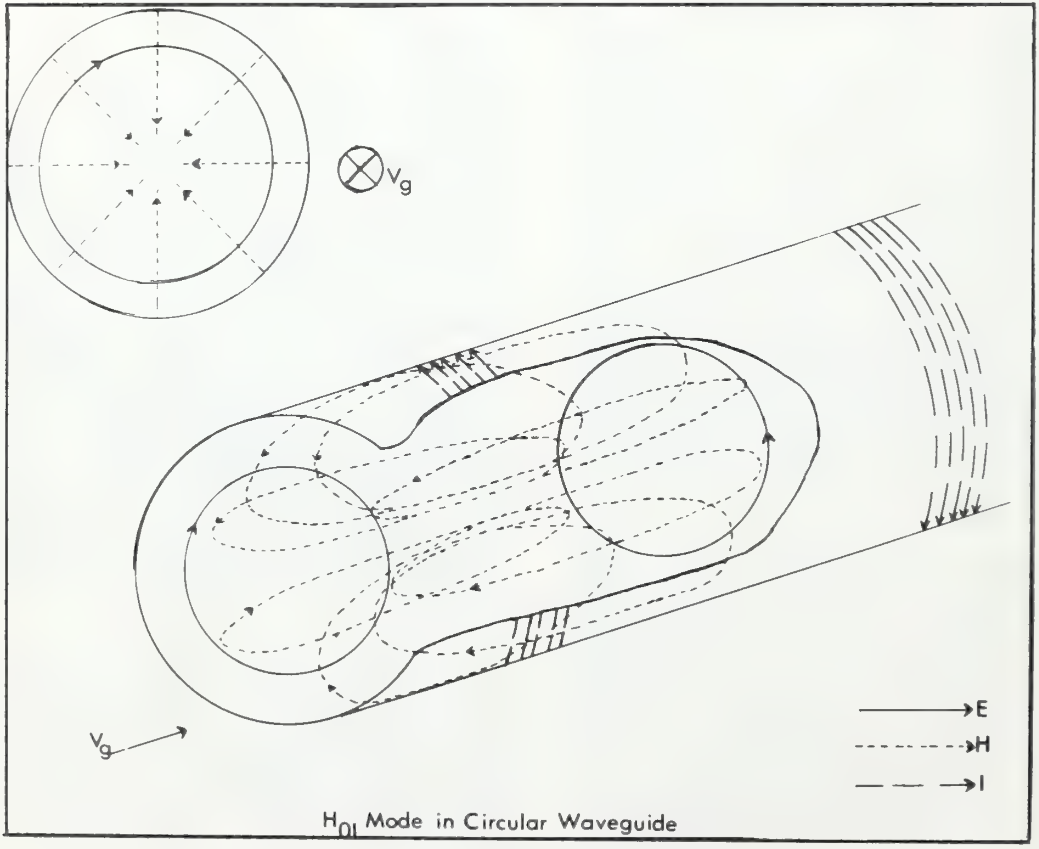

Figure 4. --E_{02} mode in hollow circular waveguide (after Mariner 1961).

frequency dependent on only one dimension, that of the radius; the other dimensions are not required to fit any half or whole wave configuration. In calculating the E_{01} mode, the resonant frequency and radius of the resonant cavity fit the formula where $\lambda \underline{c} = 2.613\ \underline{a}$.

Whenever we use this formula to calculate the resonant frequency for antennal sensilla, labial spines, or larval spines (fig. 5), we always end up in the IR region, invariably in the region of intermediate (IIR) or far infrared (FIR) between 1.5 μ and 18 μ. These calculations are used as an example and not as fact because exact configurations are not known. Measurements are at present being made with an electron microscope. The transfer of energy from the spine transducers to the central nervous system would obviously involve no image conversion, but the signal could be used effectively in the same manner as a loop antenna in the radio frequencies. In such a system there would be either a null or a reinforced signal strength, depending on the position of the paired antennae in relation to the signal.

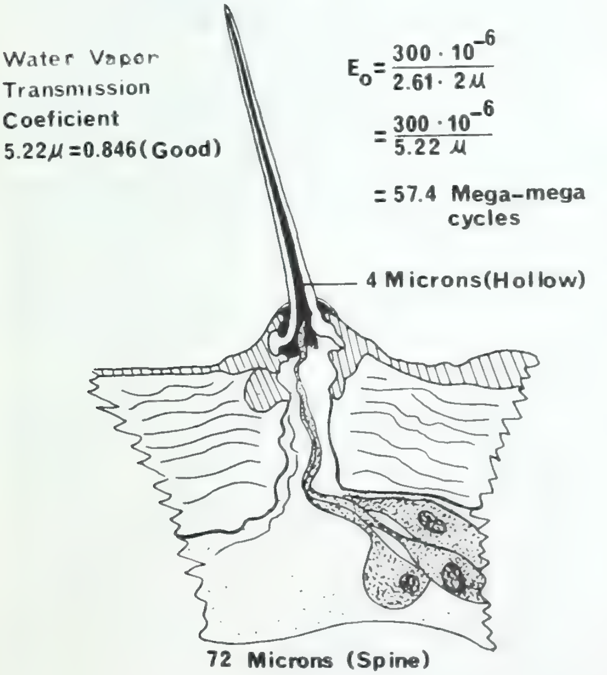

Figure 5.--Typical measurements from insect spine and calculations of E_0 mode. Transmission efficiency of this calculated frequency depends on water vapor transmission coefficient at resonant frequency.

With regard to image conversion, the obvious area of interest is the compound eye. Callahan (1965c) showed that visible, and especially shortwave, ultraviolet light quickly day-conditions the eye of the corn earworm moth (Heliothis zea (Boddie)). The eye of this moth is ideally suited for experiments, because the change from a daylight-adapted green to a totally dark-adapted black can be followed throughout its transformation. At full moon, for instance, the eye is neither green nor totally black with the central mirrorlike glow, but is instead an in-between murky, brownish color.

Callahan (1965c) postulated that the night-adapted eye becomes an IR optic-electromagnetic radiometer, since the corneal lens appears to function as an achromatic doublet and the crystalline cone as a quarter-wave, dielectric, coated field lens. During dark adaptation, the crystalline cone is coated with a pigment that in thickness is a quarter-wave of its diameter. The tracheal tapetum may well be an IR-collecting mirror.

Mazokhin-Porshnyakov (1963) showed that certain night-flying moths are color blind under very low light intensities, but have color perception at high crepuscular intensities. The electroretinogram (ERG) of day-adapted moths under relatively strong light (several tens of luxes) was extremely small in contrast to that under low light conditions. He obtained responses of 25 μ v. from a dark midnight sky, with the ERG reaching 10-15 mv. when illumination was in the order of 15 lux from an electric bulb. Mazokhin-Porshnyakov interpreted his data in terms of reflected illumination from the night sky.

This, I believe, was a misinterpretation of the data insofar as visible light was concerned. I believe that this work reinforces my hypothesis that the night-adapted eye is an IR detector. It seems to me that the insect eye is dependent on the type of radiation it receives from incandescent point sources of light, and that its wavelength sensitivity is entirely a relative phenomenon dependent on incandescence in nature, whether or not the incandescence is from the sun at daylight, or a corn plant, or another moth at night. Thus, the sensitivity of the insect eye could be compared to an incandescent lamp and rheostat (fig. 2).

In bright daylight the pigment of the ommatidia is dispersed and protects the "instrument" from the excessive IR radiation of sunlight. As evening falls and incandescence is reduced, just as with a rheostat and incandescent lamp, the visible (hot) incandescent disappears but longwave (IR warm) incandescent light remains. Toward the night horizon, longwave radiation is emitted from a deep layer of air and water vapor, where the sharpest intensity increase occurs at low elevations. The horizon, therefore, behaves like a true blackbody at its ambient temperature. All other objects in nature would be either hotter or cooler than this blackbody background and thus would be either lighter or darker to an IR detector.

Mazokhin-Porshnyakov's high value for his ERG, obtained when he oriented the moth's eye to the midnight horizon, might have been due to the IR radiation of the dark midnight horizon and not to the low-intensity reflected visible light at all. The spectral energy of such wavelengths in the 10-μ region is far greater than the small radiation remaining from the scattering of sunlight by air molecules and other particles.

It would seem to me that an instrument designed to detect the nighttime IR incandescence or IR reflected light of other moths and plants would be much more useful than one designed to detect objects illuminated by extremely low-intensity reflected visible light. The latter instrument would seem to be a particularly ineffective nighttime visual apparatus for detecting radiations if the insect has poor visual acuity, as many of the workers who have studied insect vision maintain (Dethier 1963).

The work of Smith and Kimeldorf (1964) showing a high bioelectrical response of the noctuid eye to beta-radiation, as well as my own work with ultraviolet light (Callahan 1965c), serves only to reinforce my belief that the moth eye is an IR detector at night. The shorter the wavelength, the faster the eye "light adapts" (i.e., shifts toward the short wavelengths and away from the longer IR wavelengths). The strong d.c. bias demonstrated by Burtt and Catton (1964) in noctuid eyes would certainly be expected of an IR image-conversion instrument, especially in a sensitivity instrument with the ability to shift its wavelength sensitivity back and forth along the spectrum.

In my opinion, the dilemma of the moth when confronted with incandescent light is caused by emissions of visible light from the lamp as well as tremendous amounts of IR energy (fig. 1). The moth is in the same dilemma when confronted with blacklight and mercury lamps (table 2). From a distance a moth might start for such a point source, attracted by the intense longwave IR output. As the moth moves toward the light, the intensity of the source is quadrupled as the distance is halved, causing its eyes to gradually become light-conditioned and to move along the spectrum toward a visible or ultraviolet sensitivity. Thus, the moth's eyes would never be in a static condition. The spectral sensitivity at any one moment would depend on the distance from the point source and the flight speed of the insect approaching the source. If the moth flew close enough, it would, in a sense, be sitting in the light of a small sun, and after a time its eyes would become completely daylight-conditioned. Its eyes would thus have shifted from longwave IR detection to shortwave detection of visible light. The eye pigment would have dispersed from the

Table 2.--IR lines in low-pressure mercury arc-argon daylight and blacklight tubes

Microns	Atmospheric transmission
1.01398......	...
1.12866......	...
1.35703......	Peak of tungsten filament at 2200° K.
1.36728......	...
1.39506......	...
1.52952......	Good atmospheric transmission.
1.69202......	Do.
1.69419......	Do.
1.70727......	Do.
1.71099......	Do.
1.81307......	Poor atmospheric transmission.
2.24929......	Excellent atmospheric transmission.
2.32542......	Do.
3.9400.......	Do.
4.0200.......	Do.
2 to 15......	Secondary emission.

crystalline cone (field lens) and along the ommatidia to protect the sensitive instrument from the tremendous output of IR associated with the incandescent or mercury lamp.

In any measurement of eye sensitivity, we would have to take into consideration this continuous shift from one end of the spectrum to the other. The visible part of the spectrum covers only 1 octave, but the IR covers 17 and the ultraviolet 6 octaves. The human eye covers only the single visible octave. The complexity of a moth's eye in covering 24 octaves staggers the imagination!

A system of nighttime vision would certainly be greatly affected by the moon. Not only does a full moon with its visible light partially light-condition the eye (Callahan 1965c, table 2), but also, like the incandescent lamp, it emits tremendous amounts of IR radiation, although the latter may be blocked by the O_3 band around the earth (Pettit and Nicholson 1930).

In our search for IR detectors, a third insect organ requires investigation. Histological preparations of the adult and larval corn earworm ocelli indicate that morphologically the ocelli of both stages have the configuration of an IR immersed detector. The domed cornea of the adult ocellus measures 28 μ across by 22 μ vertically. The rhabdomeres are 28 μ across by 10 μ deep. An immersed detector has a small active receptor mounted at the center plano part of a domed lens. Therefore, the ocellus would be ideally suited as an immersed detector for pickup of IR radiation from large, close sources, e.g., a plant or plant parts. Since the optic is a total unit, there would be no particular reason to assume that the IR source could be scanned by the organ either mosaically or mechanically. The behavior of many lepidopterous larvae in scanning with the head from side to side could indicate a search for incandescent or reflected point sources of IR plant radiation.

SOME EXPERIMENTAL EVIDENCE OF TRANSMISSION AND DETECTION BY MOTHS

To test some of my theories, I conducted some preliminary experiments. A behavioral characteristic of both noctuid and sphingid moths is the "warmup" of wings before flight (fig. 6). Among the noctuids, such behavior does not necessarily always precede flight and is often accomplished without regard to flight. A female corn earworm moth invariably vibrates her wings during courtship. Wing vibrations are accompanied by a tremendous generation of heat and thus by a high FIR signal.

To record this signal, I had the company manufacturing the Barnes ® IR bolometer (fig. 7) focus the IT-2 model to a distance of 10 inches. A small 29-gage hypodermic thermistor probe was inserted in the intersegmental membrane between the mesothorax and the metathorax of the test moth, and the moth mounted on the probe in front of the bolometer sensing head (fig. 8). The hypodermic probe was connected through a telethermometer amplified to the bottom vertical display of a dual-beam oscilloscope. The IR bolometer, with a field of view of 0.54 inch^2 at 3° spread, was aimed at the moth's thorax. The output of the bolometer postamplifier was connected to the top vertical display of the oscilloscope. In several of the experiments an air probe was connected to the bottom display beam for a check on the background ambient temperature of the laboratory. As the various moths vibrated their wings, their internal thoracic

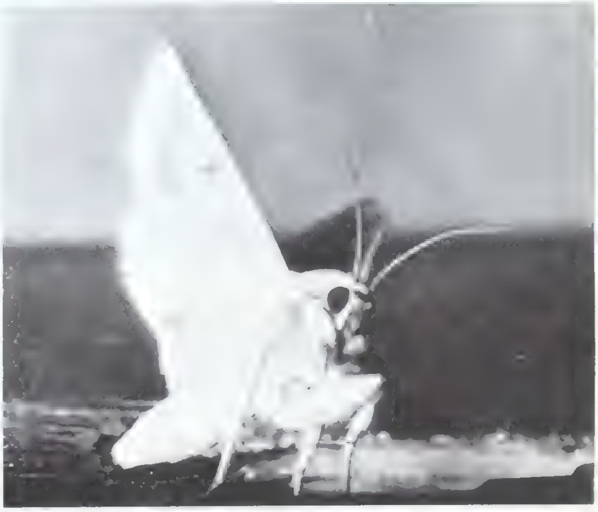

Figure 6.--Corn earworm moth vibrating its wings just prior to takeoff. This flight vibration has high wing stroke amplitude compared with low amplitude vibrations often observed in resting moths with wings held rooflike over back. Both types of wing vibration probably enter into FIR signaling and detection.

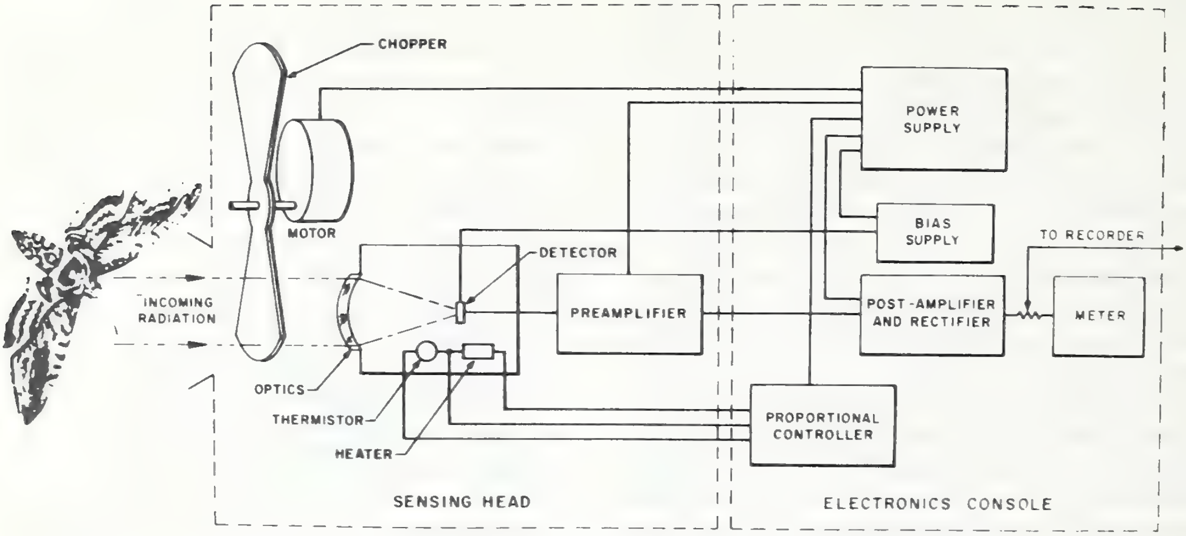

Figure 7.—Block diagram of Barnes Engineering Infrared Bolometer®. Instrument reads out directly in degrees Fahrenheit temperature.

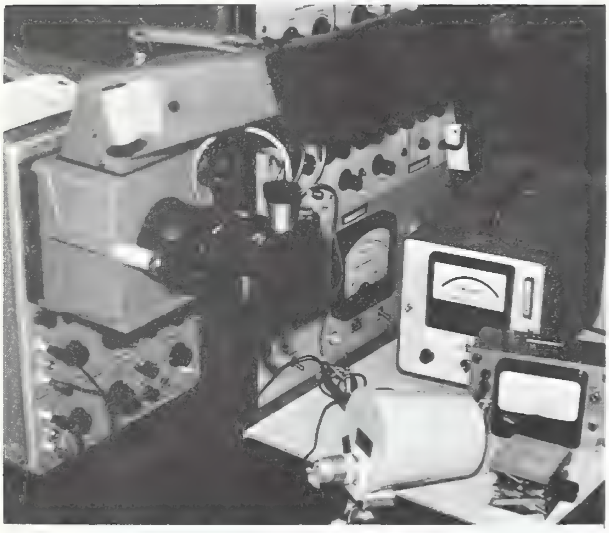

Figure 8.—Barnes Engineering Bolometer® sensing head pointed at noctuid moth mounted on small thermistor hypodermic probe. Oscilloscope recordings are made on dual-beam oscilloscope both of internal temperature and FIR emission of moth.

temperatures were recorded from the thermistor probe on the lower beam and their IR emission from the bolometer on the upper beam.

The thoracic temperatures for the various species and the λ m (FIR emissions) of the moths are given in table 3. The highest emission was recorded from the sphingid Epistor lugubris L. This is a large, thick-bodied, very dark species. The lowest recording was from the much smaller noctuid armyworm moth (Pseudaletia unipuncta (Haworth)). Since the noctuid species filled only half or less of the resolving power (area) of the bolometer sensing head, this result was to be expected.

The emission of the moth Herse cingulata (F.) above the emission of the background temperature is shown in figure 9, top. Figure 9, bottom, shows that as the bolometer was moved in a circular pattern around a moth, the maximum output was obtained from the side of the thorax off the "shoulder" of the moth. Inasmuch as the bolometer has maximum pickup for a source with an emissivity (ϵ) of 1.0, the high signals received indicated that moths have an emissivity near unity (1.0). Calculated peak frequency (fig. 9, top) for the sphingid moth H. cingulata was 9.25 μ at 39° C., or 15° above the laboratory temperature of 24° (9.75 μ). The laboratory temperature, as measured by an air probe, is shown as the solid line (24°) on the oscilloscope. The calculated energy for H. cingulata at 39° (oscilloscope recording), considering the moth thorax as a 1-cm.^{2} source with an ϵ of 0.95, would be 5 x 10^{-2} watts/cm.^{2}. At a distance of 1 km., this value would translate to an incident energy signal of 1.6 X 10^{-12} watts/cm.^{2}, energy easily detectable by a receiver. This frequency is in the middle

Table 3.--FIR peak emission (λ m) from species of Noctuidae and Sphingidae and background laboratory temperature

Species	λm (μ)	Temperature (°C.)[1] bolometer	Hypodermic probe (°)
Noctuidae:			
Heliothis zea (Boddie)....................	9.56	30	32
Pseudaletia unipuncta (Haworth)...........	9.59	29	31
Sphingidae:			
Epistor lugubris L........................	9.10	43	44
Herse cingulata (F.)......................	9.25	40	41
Xylophanes tersa L........................	9.34	37	38
Background laboratory temperature.........	9.75	24	--

[1] Temperature for noctuids, as measured by probe, was usually 2° C. higher than temperature (emission) as registered on bolometer; there was 1° difference in sphingids. Differences were attributed to bolometer being focused at 10 inches for a 0.54 inch^2 field of view at 3° spread. At this distance and spread, noctuids filled only half and sphingids three-quarters of resolved area.

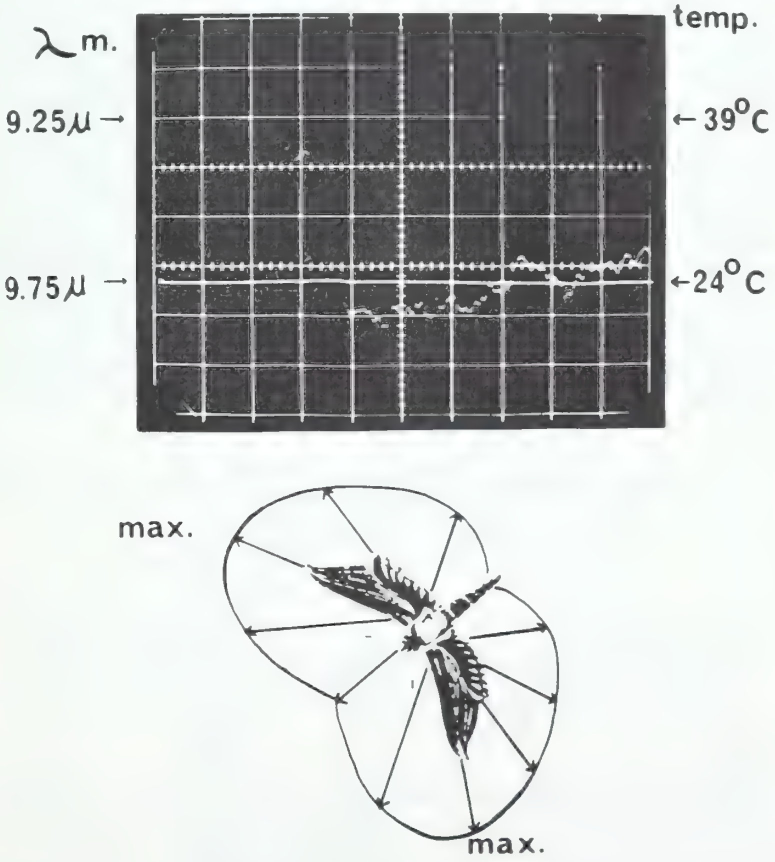

Figure 9.--(Top) FIR emission from Herse cingulata (F.) (1 sec./cm., 10 mv./cm.); emission drops from peak at 9.25 μ to background emission of 9.75 μ (solid line air probe) as moth is moved from in front of bolometer sensing head. (Bottom) Maximum radiation from vibrating moth is approximately 10° off "shoulder" of moth's thorax.

of the 8- to 13-μ. atmospheric window (Callahan 1965b). Moth frequencies transmit well through the atmospheric windows (tables 4 and 5).

Okress (1965), in reviewing unpublished research by the author, stated, "It is appropriate to mention that, you do not seem to be cognizant of the (little known) fact that even black body radiation has coherence in a sufficiently small space-time domain. This may be an important consideration because application of waveguide and resonator theory imply coherent electromagnetic fields. As a matter of fact, microwave, millimeter and submillimeter electromagnetic radiation is generated essentially coherent. This does not mean that noncoherent electromagnetic energy cannot be propagated in a suitable dielectric waveguide or stored in a suitable hollow metallic or dielectric resonator. However, for the sake of any preferred mode stability, especially in oversized waveguide, the coherence property is important."

It should be noted (fig. 10, a to f) that when wing vibration stops and frequency emission drops off, the internal thoracic temperature drops faster than the FIR output from the thorax (b and c). Thus, the IR signal and thoracic temperature are together at λ m (a), but diverge as the wing vibrations cease. The thoracic temperature drops quickly toward the ambient temperature (d). If vibrations start again, as shown in figure 10, e, the thoracic temperature rapidly closes toward the IR λ m, and both thoracic temperature and IR signal increase simultaneously (f). From these recordings, we see that the FIR signal maintains maximum power longer than the thoracic temperature. There are indications of an excellent coded signal system in these recordings.

In order to test the hypothesis that moths not only transmit FIR radiation but are also attracted to it, a 12-foot^2 room was painted black, sealed from all extraneous light, and the temperature controlled at 69° F. A blackbody, consisting of a 4-watt mercury arc-argon discharge tube wrapped in black tape, was located in the center of the room. This source emitted in the 9-μ region. No visible light was detectable. Stickum® was smeared on boards on either side of the blackbody as a trap for the moths. One hundred corn earworm moths were released in the darkroom, which was kept in continuous darkness during the experiment. Fifty-two moths were trapped on the Stickum® boards at the blackbody radiator (fig. 11, instruments removed during experiment). The moths were trapped in a semicircular pattern along the axis of the radiator, indicating that they had oriented to the λ m of the emitter. No moths were taken on a dummy check. Later the blackbody was scanned with the IR bolometer to determine the output pattern. Figure 12 shows the total catch plotted and the characteristic landing pattern, with a maximum catch along the four lobes of the emitter.

A further experiment was conducted to eliminate the possibility that the Stickum® was attracting the moths. A box 3 feet long

Table 4.--Wavelength (λm) and energy output of blackbody radiation pattern compared with those of corn earworm moth radiation

Radiator	Wave-length max. μ	Temperature (°C.)		Watts/cm^2	Incident energy in Watts/cm.^{2} source at 1 km.	Photons/ sec./cm.^{2}	$\frac{W}{W\ \text{max.}}$ factor of energy at corresponding earworm wavelength
		Probe	bolometer				
Blackbody center...	9.25	39	39	5.5×10^{-2}	1.6×10^{-12}	4.7×10^{18}	0.995
Blackbody lobes....	8.90	52	52	6.4×10^{-2}	2.1×10^{-12}	5.1×10^{18}	.990
Corn earworm thorax	9.45	32	30	4.7×10^{-2}	1.4×10^{-12}	4.2×10^{18}	1
Background.........	9.80	21	21	4.0×10^{-2}	$.8 \times 10^{-12}$	3.8×10^{18}	.993

Table 5.--Percent transmission of mercury vapor line emission and plant, moth emission at 3 path lengths (path lengths after Holter et al. 1962)

Path length	Temperature (^{o}F.)	Relative humidity (percent)	Precipitable water (g./m.^{3})	Percent transmission at wavelength (μ)								
				Lamp having indicated intense mercury vapor lines					Corn ear-worm (9.45)	Corn plant (9.4)	Water (6.2)	Incandescent λ secondary emission (8-13)[1]
				1.01	1.13	1.37	3.94	4.02				
1,000 feet	37	62	0.11	100	75	22	100	100	100	100	0	100
3.4 miles.	34	47	1.37	57	20	0	68	48	70	70	0	65
10.1 miles	40	48	5.20	39	5	0	48	35	27	27	0	40
1,000 feet	79	--	.57	99	50	0	100	100	100	100	0	100
3.4 miles.	78	73	9.40	54	3	0	82	80	64	64	0	40
10.1 miles	69	53	15.10	59	2	0	65	40	45	45	0	25

[1] Average.

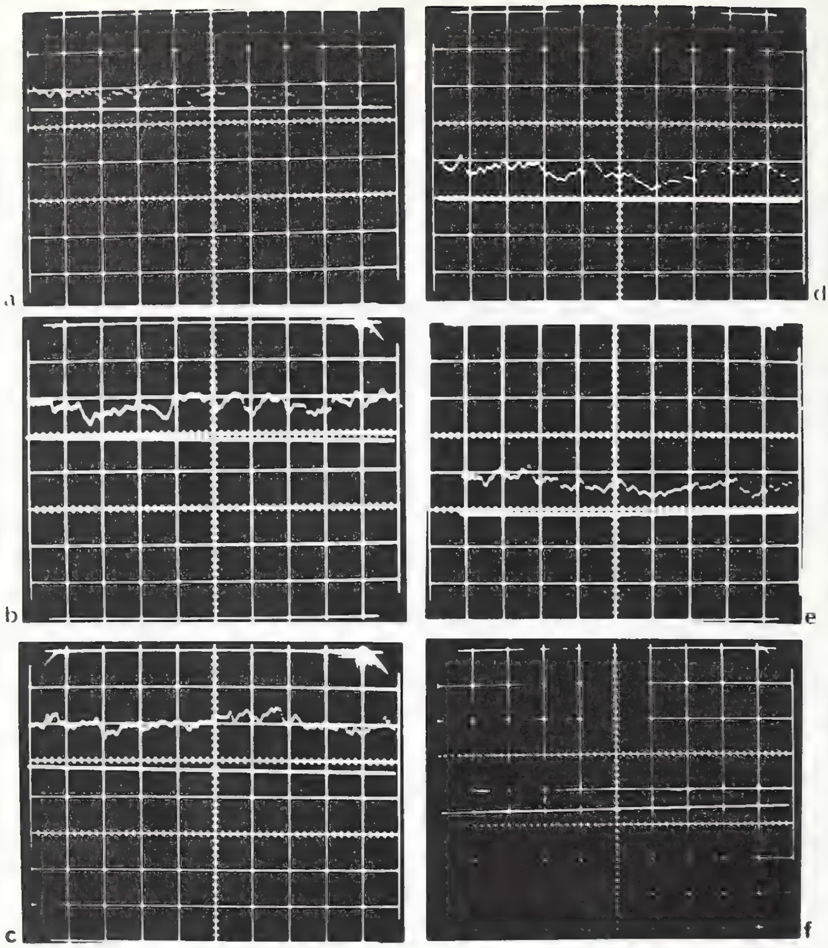

Figure 10.--FIR emission of Herse cingulata (F.). Jagged line is FIR emission, solid line is internal thoracic temperature. (a) Peak of emission at 39° C. (9.25 μ); (b) dropoff as wing vibration ceases; (c) FIR emission remains high because of heating of exoskeleton while internal thoracic temperature drops quickly; (d) internal temperature is almost at room temperature of 24°, with external FIR temperature now dropping and closing gap; (e) moth starts to warm up again (note slight curve of internal temperature line as wing frequency starts up); (f) internal temperature and FIR emission climb together as wing vibration continues.

was constructed with a shelf and a window at either end. A silver chloride filter (3 to 30μ) with a blackbody emitting behind it was placed at one window. At the opposite window was a dummy check. So as to indicate visits to either end of the box, a piece of black paper was placed on each shelf in front of the opposing windows. The criteria for visits were counts taken at various times during the dark period and the number of scales left behind on the black paper by moths visiting each end of the cage. This system was employed to eliminate any light that would result from using photoelectric counters. Results were overwhelmingly for the end containing the silver chloride filter with the IR radiator. Only a few scales had been deposited on the dummy check shelf, whereas the shelf with the emitter was completely covered with scales as well as defecation from the visiting earworm moths. During the week, 30 visits to the blackbody emitter were observed but only 1 to the opposite check.

These experiments are considered as valid proof (1) that night-flying moths generate considerable FIR radiation in the 9-μ region and

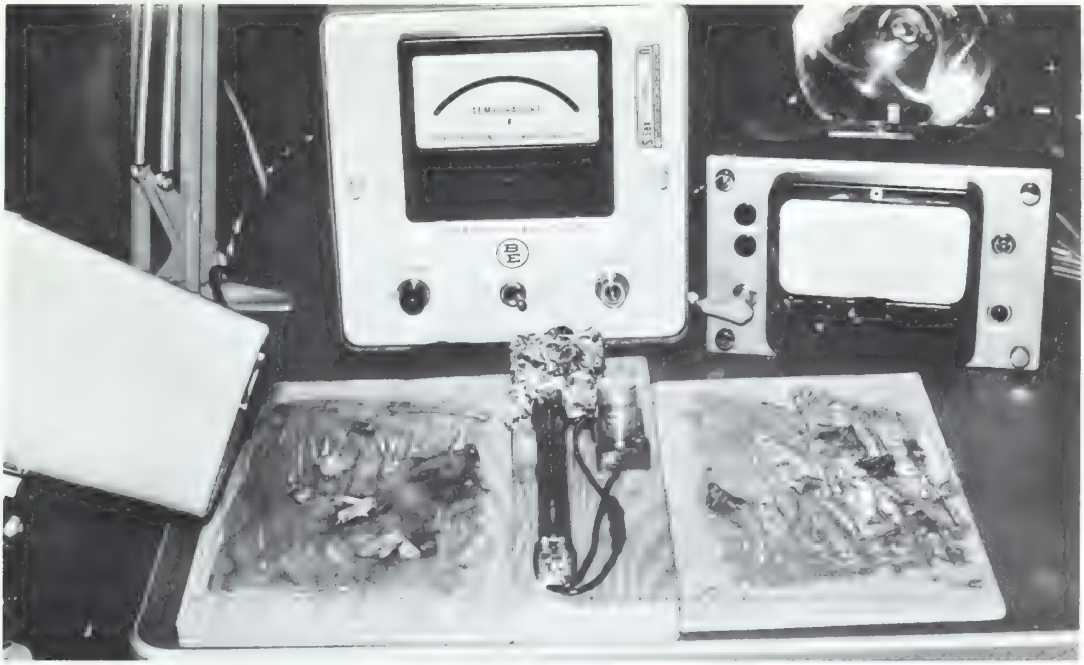

Figure 11.--Sensing head of bolometer pointing at blackbody emitter. Moths were trapped on either side of emitter with Stickum ® in totally dark room.

(2) that they can locate minute thermal sources of FIR radiation in total darkness. They would, therefore, be detectable to each other as thermal points of FIR radiation against the cool ambient background of nighttime temperatures.

Experiments were conducted with a Nernst® glower source, having a wide radiation spectrum in the IR region from 1 to 30 μ. The glower was used to irradiate eyes and antennae of moths. High-intensity IR at a thermal parameter of 120° F. focused into the eye killed the moths in an average of 60 seconds. Low-intensity IR at thermal parameters of 85° to 92° between 3 and 30 μ, focused on the antenna or eye, elicited various flight, antennal, and sexual responses at thermal parameters of 85° to 92°. Low-intensity IR at a thermal parameter of 92°, focused on the ocelli of larvae, elicited fecal pellet deposition as well as searching and head scanning by the larvae (Callahan and Cox 1965).

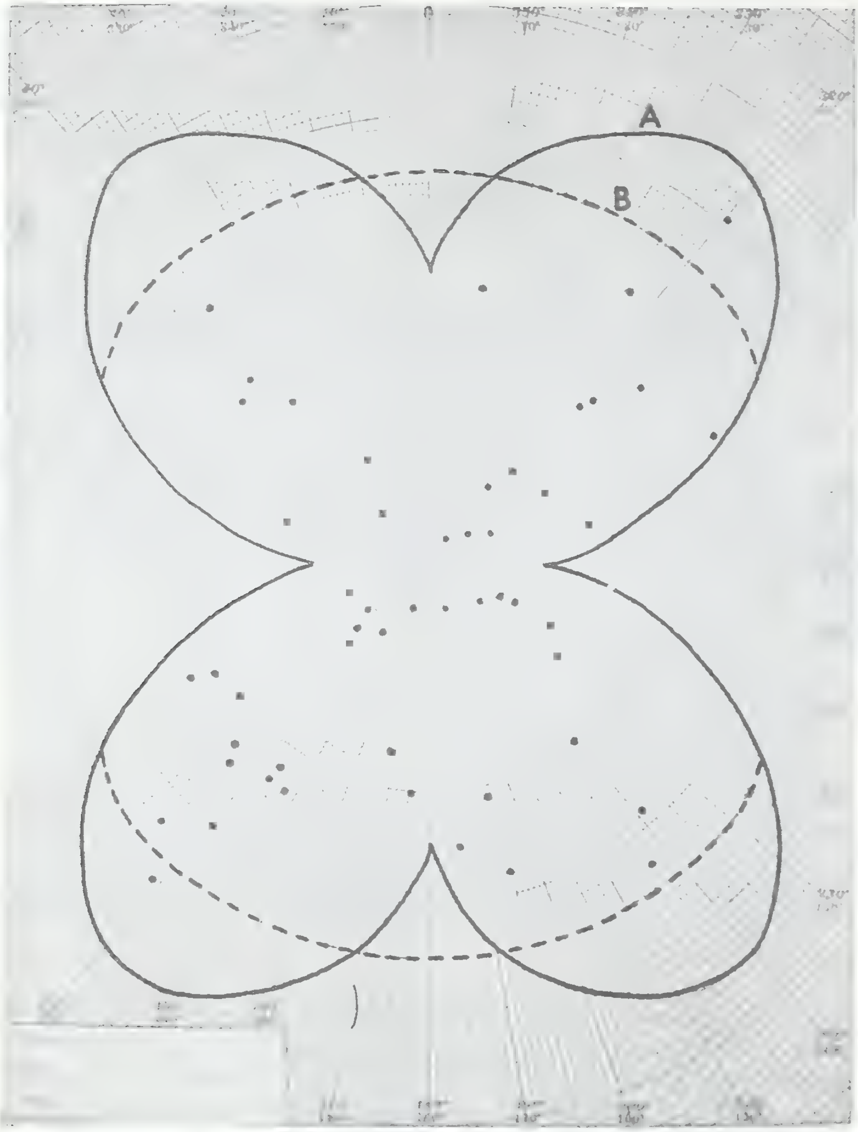

Figure 12.--Landing pattern of 52 corn earworm moths (Heliothis zea) attracted to blackbody radiator (8 to 13μ) in 12-foot^2 darkroom. (A) Radiation pattern of blackbody; (B) visible radiation before mercury arc-argon discharge tube was blacked out by heavy rubber tape.

IR ENVIRONMENTAL AND HOST PLANTS

Tanner (1963) pointed out that the thermal radiation emissivity of green plants is high--0.95 to 0.97 (table 1)--and thus measured radiation can be converted to the temperature with little error. Plants are normally warmer than the air during the day and cooler at night. This is, of course, a generality, for the strong thermal and solar exchange that occurs during the day changes considerably at nighttime. Tanner's data (1963) indicated that plant temperature may be considerably different than air temperature. Alfalfa fields measured 5° to 10° C. below air temperature at night and 5° to 10° above during parts of the day. Measurements by Valli et al. (1964) indicated that the temperature of parts of the corn plant varied over a 24-hour period. The temperature of the corn ear silk, for instance, measured 1° to 3° higher than the ambient air temperature at both 7 p.m. and again at 2 a.m. These periods coincide with the periods of maximum corn earworm activity (Callahan 1958).

Consider the following three factors: (1) The peak wavelength of a black night sky is at a maximum in the 10-μ region; (2) green plants have an extremely high emissivity and could thus emit as tremendous incandescent sources; and (3) the emissivity of a plowed field (table 1) is extremely low and could reflect considerable IR radiation. The only conclusion that one can reach is that a freshly plowed field with young corn plants might present contrasting shades of light and dark radiation resembling that of a lighted city to the occupants of an airplane. To a moth having an eye operating as a nighttime IR detector, especially if such an eye can detect a range from 1 to 18 μ, the cornfield might present a remarkable pattern for identification. If the moth flies high, the case for IR plant detection becomes even stronger, for it then could detect row after row of plants with high IR incandescence at an emissivity of 0.97 against a freshly plowed field with a contrasting emissivity of 0.28.

There is no longer any doubt that sphingids and noctuids fly at a height between 20 and 150 feet. Releases of 9,000 corn earworm moths color coded with phosphorescent powders produced a return catch of 18 moths in a blacklight trap. The moths were released at 1/4, 1/2, 1 mile, and 2 miles. The farthest releases were in areas with pine forests between the release point and light trap. All return catches were taken at 4 a.m., within 9 hours of the previous evening's releases. Immediately on release, moths that flew at all flew to heights ranging between 25 and 150 feet.

Roeder and Treat (1961) obtained flight photographs of night-flying moths avoiding bats and only a few appeared to be flying at the level of a corn plant. I have watched sphingid moths through binoculars "homing-in" from above 100 feet or so on our night-lighted greenhouse. Activity recordings in the laboratory indicated that although noctuids were relatively inactive during the night in which they emerged, most of their flight activity took place during the first 4 or 5 nights of life. This is apparently a time of intense roaming on the part of the noctuid species.

Research by plant scientists using aerial IR photography of plants has shown that the mesophyll layer of a leaf reflects considerable IR radiation. Reflection is reduced in diseased or dried leaf tissue and the difference can be detected by infrared film. The radiation emission and reflection of IR from a sick or dried plant would change so drastically that, in my opinion, the change might well account for increased attraction of moths to healthy plants. It is a well-established fact that when it has a choice, the corn earworm seeks fresh silks and avoids dry silks for oviposition.

IR ENVIRONMENT AND HOST PLANT RESISTANCE

My theories of the insect environment raise some interesting questions in regard to host-plant resistance. Does a resistant plant generate a significantly different IR emission or a significantly different IR reflection than a susceptible plant?

Figure 13 compares an IR tape blackbody, a corn leaf, and the silk of a susceptible and a resistant variety of corn. The analyses

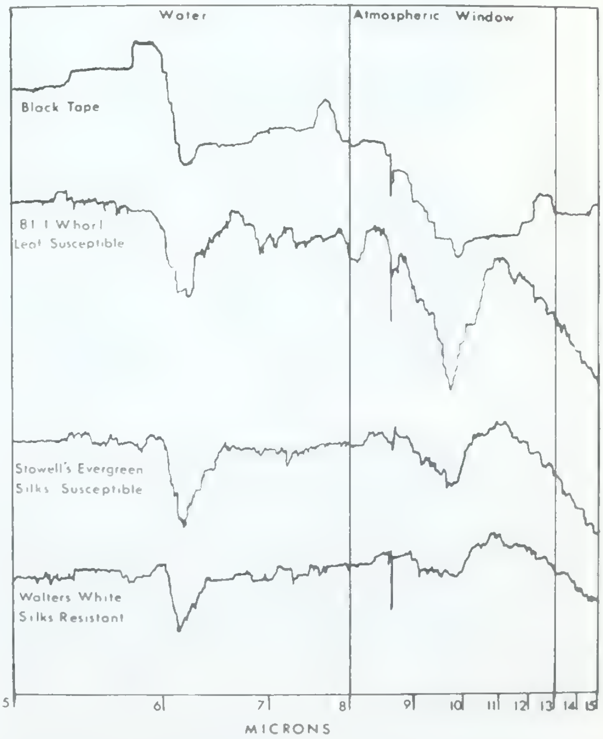

Figure 13.--IR spectrum of black tape blackbody and leaf and silks of some corn varieties. Note that silk from susceptible variety has stronger absorbance in 9-μ region than silk of resistant variety. These bands are in 8- to 13-μ window.

MICRONS

Water Vapor Transmission Coeficients

2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	5.1	5.3	5.5	5.7	5.9	6.1	6.3	6.5	6.7	6.9	7.0
930	361	689	900	950	988	997	998	997	991	970	950	930	885	792	617	361	141	260	552	164	322	416	532
902	196	571	860	930	983	994	997	994	984	958	930	902	839	707	479	196	044	112	401	049	162	250	377
844	040	369	779	888	973	991	995	991	975	932	888	844	747	555	261	040	001	012	182	002	037	068	161
782	004	205	692	843	962	988	994	988	972	905	743	782	649	406	110	004	0	0	060	0	002	010	048
695	0	073	574	779	946	982	991	982	950	866	779	695	519	239	035	0	0	0	008	0	0	0	005
536	0	005	375	658	915	972	986	972	937	790	658	536	308	062	0	0	0	0	0	0	0	0	0
381	0	0	210	531	881	960	980	960	910	707	531	381	149	008	0	0	0	0	0	0	0	0	0
216	0	0	076	377	832	944	972	944	873	595	377	216	041	0	0	0	0	0	0	0	0	0	0
064	0	0	005	161	736	911	956	911	800	400	161	064	001	0	0	0	0	0	0	0	0	0	0
005	0	0	0	048	635	874	937	874	722	235	048	005	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	005	502	823	911	823	615	093	005	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	287	724	860	724	425	008	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	133	616	802	616	260	0	0	0	0	0	0	0	0	0	0	0	0	0	0

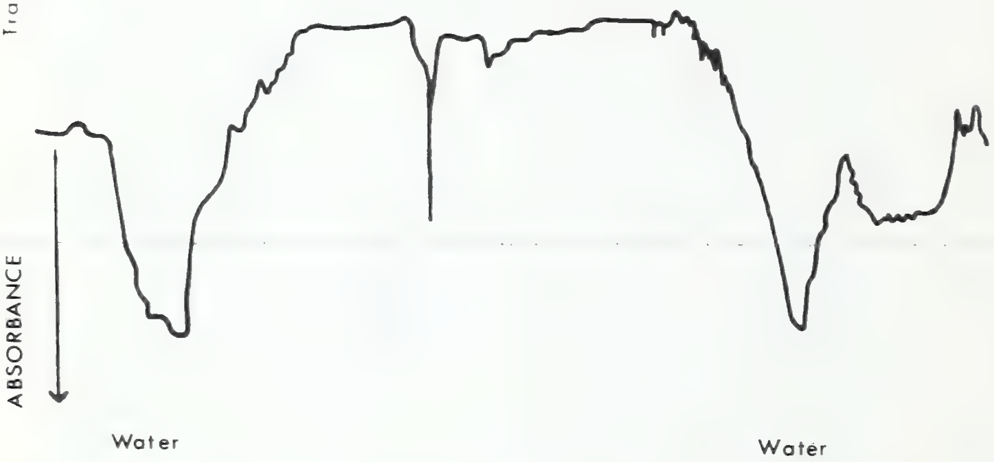

Figure 14.--IR spectrum (2.5 to 7 μ) of piece of exoskeleton from sphingid moth. Two major water absorption bands of plant or animal tissue would not transmit well because these frequencies have low transmission coefficients. 2.9 μ would transmit better at 0.689 than 6.1 μ at 0.260. Water vapor coefficients are in decimal parts of 1.0, where w = precipitable water, cm. at sea level (table after Hackforth 1960).

were made with a Perkin-Elmer ® Model 237 Spectrophotometer, with an attenuated total-reflectance accessory. This attachment permits analysis of solid samples without control of the sample thickness. If in figure 13 we consider the 8- to 13- μ window, where good atmospheric transmission occurs, we note that the absorption signal was somewhat stronger in this window for the silk of the susceptible variety than it was for the resistant variety. If, because of some chemical or physiological factor, IR emission is different for one part of the plant than for another, the total plant may then be presenting a different pattern to the insect eye that it customarily sees.

Strong water absorption bands in the 3- and 6-μ region complicate the IR pattern, but, as figure 14 illustrates, these bands do not transmit well through the atmosphere. At 6.1 μ, for instance, the water vapor transmission is very low (only 0.260) compared with the 4-μ region (0.997) or the 8- to 13-μ window.

In spite of poor atmospheric transmission in these regions, however, water itself has a high emissivity of 0.98 (table 1) and radiates as a blackbody from 4 to 13 μ (Clark and Frank 1963). In the blacked-out room the moth of the cotton leafworm (Alabama argillacea (Hübner), which prefers moist areas, was attracted to a flat pan of water. Some 42 out of 60 released moths located and drowned in the pan in total darkness. Blackbodies of all sorts in a totally dark room seem to be highly attractive to night-adapted flying moths.

TRANSMISSION THROUGH MATERIALS

Callahan (1965d) postulated that certain of the IR frequencies may play a part in the control of diapause. The numerous spines of larvae could possibly serve as transducers to transfer radiant energy from the environment to the central nervous system of the insect. In considering the IR environment, not only are the absorption and reflection of such frequencies important but also the transmission of specific wavelengths through various materials. Thus, a leaf surface between a moth or a larva and an IR source may serve as a filter in one region of the IR spectrum or as a window in a different region. For instance, glass transmits visible radiation but blocks many IR frequencies.

Figures 15, a to i, presents oscilloscope recordings of transmission through various substances in the 9- μ region as follows: a represents the total signal from a blackbody emitter through a silver chloride filter (9.08 μ); b, the background laboratory frequency (9.75 μ); c, the transmission through a sheet of yellow tablet paper; d, a corn leaf; e, a latex glove; f, a lens paper; g, a paper napkin used in rearing; h, a wire screen; and i, the wire screen removed at the center line of the oscilloscope to show the rise to maximum temperature (9.08 μ). The reader should note that in the 9- μ region about a third of the total emission penetrates a corn leaf. Over two-thirds is transmitted through the paper napkin, which we use as a surface for corn earworm oviposition.

Table 6 (Summer 1962) gives the thickness of certain woods that can be permeated by IR radiation. Some woods freely transmit certain wavelengths and are thus open windows to such frequencies. The implications for parasites that locate wood-boring larvae are obvious. A tremendous amount of work needs to be instigated on IR transmission through the various materials found in nature.

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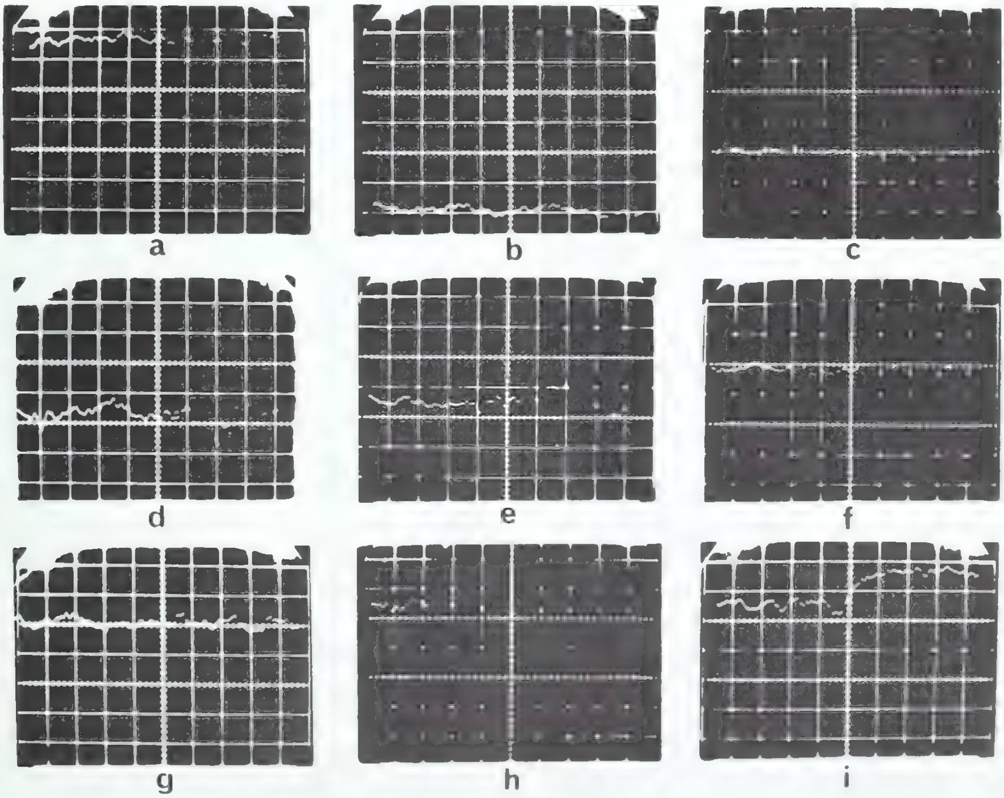

Figure 15.--Transmittance of 8- to 13-μ FIR through various materials (see text). (a) Blackbody emitter (λ max. 9.08 μ), (b) background emission (9.75 μ), (c) yellow tablet paper, (d) corn leaf, (e) latex glove, (f) lens paper, (g) paper napkin, (h) wire screen (i) wire screen removed at center line to show rise to maximum temperature (9.08 μ).

Table 6.--Thickness of wood permeable to IR radiation (summer 1962)

English name	Thickness (mm.)
Larch	5-7
White fir	6-7
Spruce	6
Alder	5-6
Lime	4-6
Pine	3-4
Poplar	4
Maple	4
Hornbeam	2-3
Beech	3
Elm	1
Oak	2
Plum tree (domestic)	1-2
Plum tree (wild)	1-1.5
White walnut	.5
Siberian pine	Freely transmitting.
Yellow pine	Do.
Yellow deal	Do.
Tasmanian oak	Do.
American walnut	Opaque.
Iroko teak	Do.
Ebony	Do.

NOCTURNAL IR ENVIRONMENT

Figure 16 illustrates my views on the night-flying moth and the IR environment. During a day with a clear sky, the moth maintains a shortwave, "light-adapted" eye and is not active. As the sun goes down, again as for the incandescent lamp and rheostat, the visible and ultraviolet decrease almost to the point of nonexistance. The longwave IR, although it may be of less intensity than the longwave rays of the sun, exists in its own right without the shortwave background interference of visible and ultraviolet light from the sun. It is precisely at this time that the moth, and indeed many insects, are stimulated to activity. It is as eminently logical that night-flying insects, whether mosquitoes or moths, should "see" or otherwise sense in this region as it is that man should develop nighttime IR instruments to aid in his nocturnal location problems.

During the early part of their lives, sphingid and noctuid moths spend considerable time randomly wandering about the countryside. During this time, individuals from even an extremely small spring population of five or six specimens per square mile would come within a 1- or 2-mile range of each other. Their proximity would be further enhanced by attraction to the host plant or into thermal pockets of optimum temperature. For such attraction to take place, weather parameters would be of supreme importance if IR is indeed a means of host and mate detection. On a cool night with low absolute humidity (13 g. of H_20 per m^3 at 80 to 90 percent RH), IR transmission, especially through the IR windows, would be excellent. In spite of the presence in the area of a light trap with high power, plant emission could lure the moths.

Suppose, on the other hand, the night were extremely warm, with high absolute humidity (26 g. of H_2O per m^3 at 80 to 90 percent RH), the moth might still randomly wander. There would be no danger of desiccation at the high RH in either situation. In the second situation, however, the excessive number of water molecules and higher temperature would not only reduce the efficiency of the IR window but would also reduce the difference in IR emission between the plant and the background or that between the vibrating moth and the background. More moths might thus be collected at the light trap, which would be emitting tremendous amounts of IR radiation.

The pitfall in this reasoning is, of course, the relativity of all things. Thus, during late summer periods when moth populations were extremely high, one might get more moths in the light trap at lower temperatures than at higher temperatures for the simple reason that with optimum weather conditions a greater part of the very high population would be flying around and spatially more moths would be close to the trap. The problem might be further complicated by one particular moth having at any one moment a slightly different eye configuration than another moth, simply because one moth might be facing the light from the trap and another moth facing away from the light. All these factors, no doubt, would account for the differences in catch from night to night, as well as the fact that the moths arrive at light traps in a stop-and-go pattern of activity.

Assuming that moths are attracted into an area of host-plant emission or into thermal pockets, we may further assume that both

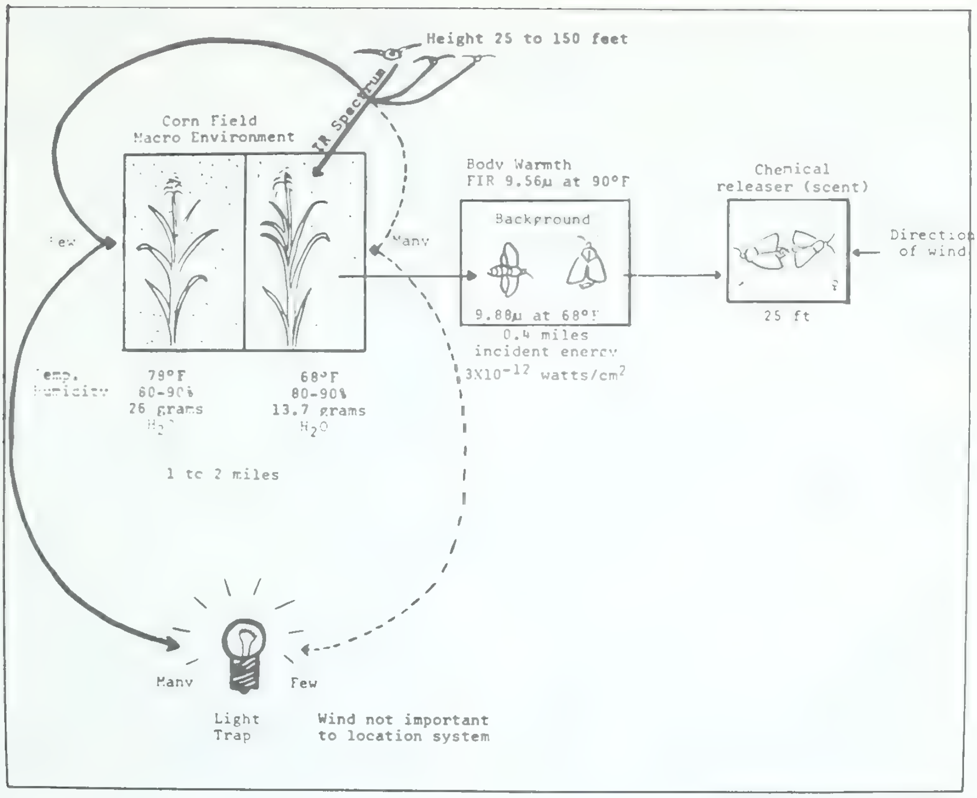

Figure 16.--Summary of my theory on night-flying moths and IR environment (see text).

sexes will certainly arrive in an area within one-fourth mile of one another. During their searching they are continuously vibrating their wings and thus producing a high thermal FIR signal. A corn earworm moth with an incident energy at 1 km. of 1.4 X 10^{-12} watts/cm^2. is emitting a detectable signal (table 4).

The oscilloscope recordings show that as moths warm up the signals go up and down. This variation is similar to that of the on-and-off signaling fireflies demonstrated in the visible spectrum. The only difference is that the fireflies signal with visible incandescent light and the moths signals with incandescent IR. Species could thus assemble not only at their host plants or in areas of thermal inversions but also in close proximity to each other. The final identification would be by a chemical releaser (scent), which would permit the sexes within the species to locate each other and initiate the clasper response. Since many noctuid and sphingid males also have scent glands, these chemical stimulators may in many species be cross-identification mechanisms (Callahan 1965b).

To summarize and in doing so to emphasize all my theories and evidence, I present the following (fig. 16):

(1) Newly emerged moths wander in random flight over the countryside at considerable heights.

(2) These moths are attracted by IR emission and reflection into areas of host plants.

(3) The efficiency of plant or moth attraction is dependent on prevailing weather parameters, which affect the IR transmission. In this regard, we might add that moths are also attracted into thermal pockets of optimum temperature. Thus, they would prefer pockets of cooler air scattered around in the warmer environment of a hot summer. This phenomenon would also enhance mate location.

(4) Moths near each other, either because a plant or a pocket having optimum thermal parameters attracts them, vibrate their wings and send out FIR signals, which are identified by the IR eye or certain tuned spines of the antennae of the opposite sex. Thus, the males and females are brought within very close range of one another.

(5) Moths identify those of the opposite sex and are stimulated to mate (clasper response) by chemical releasers (scent). In this regard, in view of the many different types of antennal and other spines, it may well be that the IR or microwave emission of scent molecules themselves is tuned in by the resonance of certain spine transducers that transfer the signal from the molecule to the nervous system (Callahan 1965b).

SUMMARY

A completely new concept of the insect environment is introduced. It is based on intermediate and far infrared frequency transmissions through infrared atmospheric windows. This concept involves the utilization of such transmitted frequencies in the life cycle and behavior of the insect. Considerable evidence indicates that host location and insect communication depend on the detection of such frequencies in the 1- to 18-μ spectrum. Frequency transmissions in the 9-μ region have been received, amplified, and recorded on an oscilloscope from moths in the families Noctuidae, Sphingidae, and Lasiocampidae. In addition, various species of Noctuidae have been attracted to a blackbody emitting in the 9-μ region in a totally dark room.

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ELECTROMAGNETIC ENERGY AND SOUND FOR USE IN CONTROL OF CERTAIN PESTS

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Future possibilities for pest control utilizing electromagnetic energy and sonic and ultrasonic energy have received more attention recently because of pesticide residue problems. It is difficult to know what practical methods may be developed using energy from the vast electromagnetic spectrum or from sonic and ultrasonic sources, but a few such applications have already proven successful. Others are being tested in the field and studied in research laboratories around the world. Significant developments in pest-control methods can be expected from this research. Some of the past accomplishments, current studies, and future possibilities for pest control using electromagnetic, sonic, and ultrasonic energy are reviewed in this paper.

ELECTROMAGNETIC SPECTRUM

Electromagnetic energy encompasses a wide range of radiation (fig. 1). All the electromagnetic radiations from the low-energy radio waves through infrared, visible light, ultraviolet, X-rays, and gamma rays are basically similar in nature. All travel through free space with the velocity of light. The relationships between wavelength, frequency, and energy of the quantum of radiation anywhere in the electromagnetic spectrum are described by the following equations:

$$\lambda = \frac{c}{\nu} \qquad \text{and} \qquad E = h\ ,$$

where c and h represent two fundamental physical constants, respectively, the velocity of light in vacuum and Planck's constant, λ is wavelength, ν is frequency, and E is the energy of the quantum or photon. Thus, as wavelengths become shorter across the electromagnetic spectrum, the energy of the quantum of electromagnetic energy increases. The energy of the quantum is frequently expressed in electron volts, a convenient energy unit when dealing with X-ray and gamma-ray radiation.

Several different units are used for wavelength depending on the region of the spectrum. Meters and centimeters are common in the radio-frequency range, whereas the micron, millimicron (nanometer), and Angstrom unit are used for the infrared, visible, and ultraviolet regions.

The effects of electromagnetic energy on living matter have been studied in detail for certain phenomena, such as photosynthesis and the absorption of ionizing radiation, but much still remains unknown concerning the interaction of all types of electromagnetic radiation with biological material. Generally, however, the longer wavelength radiations produce heating effects and the shorter wavelength radiations produce chemical effects, including ionization of the atoms of absorbing media (9).

Radio Frequencies

Interest in pest control with radio-frequency (RF) electromagnetic energy has centered mainly in studies with insects. It has been speculated that insects might be controlled by radio waves of some particular frequency, which, by virtue of some resonance phenomena or selective absorption, would be effective in killing them. So far such deadly selective frequencies have never been found, nor has any conclusive evidence been presented to indicate that anything other than high-frequency dielectric heating is involved in the lethal action of RF electric fields on insects (136). On the other hand, neither has it been conclusively shown that some specific effect other than heating cannot exist (102). Effects of heating and any specific nonthermal effects due to the electric field per se are difficult to separate. Recent attempts to do so using

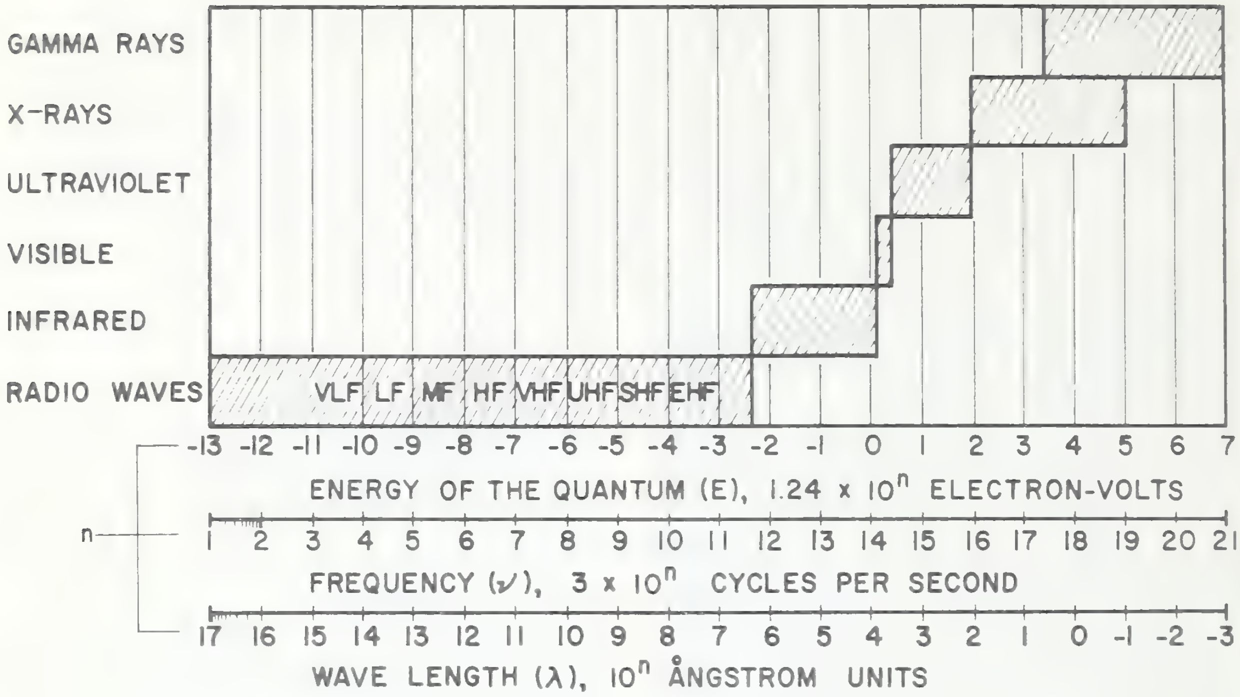

Figure 1.--Electromagnetic spectrum showing appropriate ranges of radiation.

pulse-modulated RF energy have shown evidence of effects not attributable to thermal causes by the investigators (11, 50, 71, 72, 97, 118, 135).

Based on RF heating only, control of insects by radiation of RF energy into any sizable space is impractical (10). Calculation of the power required for a special case revealed that tremendous amounts of energy are needed for a range of only a few feet, with power requirements increasing as the square of the distance from the radiating antenna. Concentration of RF energy into a narrow beam reduces the energy requirement, but it would still be substantial.

Several good reviews have been published on studies of RF electric fields for pest control (5, 56, 102, 105, 112, 136, 137, 140, 145), and important principles involved in applying this type of energy have been treated in the literature (56, 105, 136, 140, 149).

Major interest in applying RF energy for insect control involved treatment of grain, foodstuffs, and wood. The basis for this interest stems from the nature of absorption of energy by materials in a high-frequency electric field. The power dissipation depends not only on the frequency and intensity of the field but also on the electrical characteristics, more specifically, the dielectric properties of the materials involved. For certain combinations of hosts and insects, their respective dielectric properties are favorable for differential or selective absorption of energy (105, 136, 149), and the insects can be killed without damaging the host material. Thermal tolerance of the host and infesting organism may be sufficiently separated that heating by conventional means is a possible control measure. RF heating, however, can be advantageous if the pest organism can be selectively heated, because less energy is required to accomplish control. In addition, RF dielectric heating is much more uniform and faster than conventional heating.

Studies on stored-grain insect control in wheat using a frequency of 39 megacycles per second (mc.) showed that all developmental stages of several species were controlled by exposures lasting only a few seconds (105, 149). Immature forms were more resistant than adults, and differences were noted in susceptibility among species. Complete mortality of the most resistant, however, was achieved by RF treatments with resulting grain temperatures of 60^{0} to 65^{0}C. in 25-gm.

samples. These exposures were not damaging to germination if wheat moisture content was below 14 percent. Complete mortality for rice weevil adults (Sitophilus oryzae (L.)) was obtained with resulting grain temperatures of less than 38°, which indicated that selective heating of the insects was probably responsible. Higher field intensities were more effective for rice weevil adults, but influence of frequency and field intensity on general effectiveness of treatment was not clearly determined. Experimentally derived values for a differential heating factor agreed with theoretical prediction of differential heating between insects and grain due to exposure in the RF field. Costs for practical-scale treatment were estimated at 3.5 cents per bushel, which considerably exceeded costs for chemical fumigants.

Studies of wood disinfestation using RF electric fields at 37.5 and 76 mc. (137) and 2,425 mc. (141) demonstrated insect-control possibilities in structures where conventional heating and chemical methods may be impractical. The microwave frequencies appear to offer means of deeper penetration where only one side of the structural member is accessible.

Use of RF energy has also been studied in attempts to control weed seeds by heating them to a lethal point (78, 91). For economic reasons, however, RF heating would be practical only if a rapid heating process was essential or if weed seeds mixed with crop seeds could be selectively devitalized. Many factors influence the exposure required for achievement of lethal heating by RF energy in seeds (104), and favorable conditions for selective heating of weed seeds are probably not very likely.

A highly successful application of RF dielectric heating for pest control was represented by a 120-kw. installation for sanitizing feed bags (157). Bales of bags on a conveyor were rapidly heated without damaging the bags to between 104° and 116°C. to kill any disease organisms or insects that might be present. Substantial savings were effected by safely reusing feed bags several times.

Other practical applications of RF energy for pest control have not yet developed, but use of this type of electromagnetic energy certainly merits further study. Discovery of destructive nonthermal effects or other improvements in efficiency of the method could make this type of energy available for practical use. Only a narrow part of the RF spectrum has received any appreciable attention in pest-control studies. Most work has been done in the 1- to 100-mc. frequency range. There is a need to explore the remainder of the RF spectrum, particularly the higher frequencies.

Infrared

Possibilities for pest control using infrared energy have not been studied as extensively as parts of the RF spectrum, but infrared energy has been applied commercially for insect control in grain (138, 153). Grain was simply heated by radiant energy from infrared lamps as it moved on a conveyor belt and was held at temperatures lethal for insects for the required time. Radiant energy from a gas-fired infrared heater has also been used in research on insect control in rough rice (123). The lesser grain borer (Rhyzopertha dominica (F.) was found more resistant than the rice weevil, with grain temperatures of 68° and 56° C., respectively, reported necessary for control.

Mosquitoes are attracted to insect traps using regular tungsten-filament incandescent lamps. While such lamps are used mainly for lighting, they emit most of their radiant energy in the near infrared region. A 500-watt quartz infrared lamp, which emits more infrared and a smaller percentage of visible radiation, was found more effective for attracting mosquitoes than a 200-watt incandescent lamp in tests comparing traps equipped with the two different lamps (30). Longer wavelength infrared radiation from a lamp dipped in black paint, however, was found no more effective for attracting mosquitoes than a nonenergized lamp of the same type (14).

Warmth, however, is a recognized factor in attracting mosquitoes (24), and beliefs have been expressed that certain insects may locate warm-blooded animals by sensing infrared radiation. Interesting theories based on electromagnetic radiation and reception in the infrared region have been advanced by entomologists and physical scientists to explain the long-range location of the female by male moths of night-flying Lepidoptera species (31, 46, 90). Evidence offered in support of these theories is largely circumstantial or indirect and is not yet very convincing. It includes: (a) Observations of the fact that moths can raise their body temperature several degrees above ambient temperature by physical activity, such as wing beating; (b) bodies at these temperatures give rise to infrared radiation at wavelengths corresponding to a transmission window in the atmospheric absorption curve for infrared radiation; and (c) configuration and dimensions of the fine structure of moth antennae indicate that parts of the antennae might serve as infrared receptors at wavelengths corresponding to those radiated by the moths. Structure of the compound eye of the corn earworm moth (Heliothis zea (Boddie)) has also been analyzed, with the idea that it could function as an infrared receptor for detection of far infrared radiation and image formation (32).

Extensive and difficult experimental work will be required to settle the question of the radiation theory of communication in insects. If it should be confirmed, in any way, however, new control measures using infrared energy may be possible.

Infrared technology has developed rapidly in recent years because of its significance as a passive detection method and emphasis on military applications. Instrumentation for infrared research is now being developed that will permit interesting investigations relating to possible pest-control methods.

Visible and Ultraviolet

Visible radiation refers to that part of the electromagnetic spectrum to which the human eye is sensitive, i.e., the region from somewhat below 4,000 to somewhat below 8,000 Angstrom units (A.). The range of response for insects, however, extends into the ultraviolet region to somewhat below 3,000 A. (68), and, whereas human visual acuity peaks at about 5,560 A., peak response of many insects occurs in the near ultraviolet at about 3,650 A. (74, 77, 146, 148). Some insect species have shown peak responses to light in the 4,900- to 5,200-A. range (68, 74, 75, 77, 131, 146, 147, 148). In some cases, the latter range was a secondary peak, and in some the primary peak depending on light intensity. Physiological as well as physical and other factors influence the phototaxis of insects (48, 69, 88, 108, 132, 163).

There is a vast amount of scientific literature dealing with visible and ultraviolet radiation and its relation to insects. From the standpoint of pest control, insect traps using light sources as attractants are probably the best example of practical application for this type of electromagnetic radiation (64, 73, 76). Most commonly used insect light traps employ a blacklight fluorescent lamp as the attracting source. These lamps emit strongly in the ultraviolet region, with peak emissions in the 3,500- to 3,800-A. range, and attract large numbers of insects of photopositive species. Insects attracted to the lamps are trapped in a collection device, usually a funnel and container, which is mounted below the lamp. Various trap designs have been developed for particular purposes (64, 76), and numerous experiments have been conducted to determine the most attractive lamps for particular insects (17, 43, 65, 67, 83, 113, 163).

In recent years, light traps have come into widespread use as an entomological survey device, and as such have been extremely useful in overall insect-control programs. Light traps are now used extensively for detection and quarantine work (18, 66, 133). They have also been helpful in detecting population changes and in predicting potential insect infestations and need for control measures (66, 94, 109, 115, 121). Information on insect light-trap collections at various locations throughout the United States is currently tabulated and published weekly for the benefit of entomologists concerned with insect-control problems.[1]

Use of insect light traps for direct control has been of interest to a few scientists for many years (49, 64, 95, 107, 114, 127, 128, 134). Light traps afforded some protection from insect damage to vegetable crops in garden-plot studies (42, 43). In the last few years, results of a large area study on direct control of tobacco hornworms (Protoparce sexta (Johannson)) using blacklight traps have been encouraging (129). In 1962, with a trap density of three traps per square mile over a circular area 12 miles in diameter, tobacco hornworm moth populations were reduced by more than 50 percent. Further reductions were observed during the last two seasons.

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[1] Cooperative Economic Insect Report, issued by Plant Pest Control Division, Agricultural Research Service, U.S. Department of Agriculture.

Because of these promising results, light traps have been installed in several parts of the United States for field trials in controlling tobacco, cotton, and vegetable insects. Many of the installations do not include plans for scientific evaluation. At the present time, there is not sufficient evidence to assure that field installations of insect light traps will provide the desired control for any species, but indications are interesting, and additional research in these methods is certainly needed.

Possibly more important than the applied research on visible and ultraviolet radiation for insect control is the basic research needed to develop further understanding of phototaxis and the action spectra for various economic insects. Basic information of this type should point the way to development of more suitable radiant attractants and more efficient traps for use in insect control. The basic and applied research in this field should certainly be complementary and may well achieve direct practical insect-control methods of real significance.

Very recent studies indicate other possible ways in which visible and ultraviolet radiation might some day be applied for insect control. These hopes stem from observations that light exposures as brief as a photoflash during a critical time in the normal dark period can upset the life cycle of an insect (161). Such flashes of light prevented normal diapause in insects held under laboratory conditions, which simulated diurnal changes in lighting. Much more research will be needed, but, if insects could be forced to bypass their normal diapause under field conditions, control may be possible, since their "timing" would be off schedule with respect to seasonal climatic conditions.

Daily exposures of a few minutes to red and far red light were also found to inhibit in other ways the normal development of some insects (12). Photoperiodic phenomena are important aspects in insect and animal life as well as in plant life (1, 116), and as these become better understood possible control methods may be developed.

X-Rays, Gamma Rays, and Other Ionizing Radiations

X-rays and gamma rays comprise the high-energy end of the electromagnetic spectrum. They are extremely penetrating types of radiation. X-rays are emitted when orbital electrons in the inner shells of atoms near the nucleus change from a higher energy level to a lower level. Gamma rays, on the other hand, are emitted from the nuclei of radioactive materials and arise from the nuclear disintegration and other reactions. They may also result from the annihilation of an electron pair (negative electron and positron). There is an overlapping in the spectrum of X-rays and gamma rays (fig. 1). The nature of the two in this region is believed to be the same except for their origin.

Effects of X- and gamma radiation on biological material arise from ionization of the atoms in the tissues, and can be very damaging if sufficient energy absorption results from radiation exposure. Similar biological effects are produced by particle radiations, such as alpha, beta (energetic electrons), neutrons, and accelerated electrons, but they have differing penetration characteristics and mechanisms of absorption.

A considerable amount of research has been conducted and is continuing on the use of ionizing radiation for pest control. A classic example of radiation applied to solve a severe insect problem is furnished by the program that eliminated the screw-worn (Cochliomyia hominivorax (Coquerel)) menace in the Southeastern United States. The principle involved the sterilization of male flies with gamma rays from cobalt-60 and their release in large numbers to mate with normal females, which mate but once, thus producing nonfertile eggs and eventual elimination of the population (29, 80, 85, 86, 87). Similar methods eradicated the melon fly (Dacus cucurbitae Coquillett) on the Pacific island of Rota. Effects of ionizing radiation on reproductive ability of the European corn borer (Pyrausta nubilalis (Hübner)) have also been considered (142).

Application of the "sterile-male" control method is limited by certain environmental and biological factors. Control by direct irradiation appears to have wider potential application for insects that infest stored products and some other materials. Since, economically, grain is probably the most important stored product with which we have serious insect problems, the use of electron and gamma radiation for disinfesting grain has received much attention.

The findings and fundamental and applied problems of using gamma-radiation treatment are well set forth in publications by Cornwell et al. on research carried out in the United Kingdom (34, 35, 36). The effects of beta, gamma, and X-rays on stored-grain insect pests are all comparable in their lethal and sterilizing properties. Insect control is possible using any one of the three following dose levels: Doses of about 500,000 rads are reproductively sterilizing, produce death within 24 hours, and provide a high measure of control of the microflora, probably allowing grain storage at higher moisture contents. Doses of about 100,000 rads produce sterilization, death in about a week, minimize insect feeding damage prior to death, and sterilize mites. Doses of 15,000-20,000 rads provide sterilization of the insects and death of the adults in 2-5 weeks and arrest the development of immature stages. Development of the eggs and larvae of granary weevils (Sitophilus granarius (L.)) is prevented by doses as low as 5,000 rads, but complete sterilization of the adults requires a higher level of treatment.

Since radiation accelerates the mutation rate, there is a possibility with sublethal treatments that insects might develop resistance to radiation through combined effects of selection and radiation-induced variants. Most of the mutations, however, will be lethal, and development of radiation resistance has not yet been demonstrated (35, 36). Nevertheless, doses for commercial application must contain a margin of safety to insure complete sterilization. A dose of 16,000 rads has been recommended as adequate for granary weevils (38), flour beetles (13, 39), lesser grain borers, and cigarette beetles (111), but somewhat higher levels of exposure may be required for the Indian-meal moth and tropical warehouse moth (111). Moth species were also found more resistant than beetles and weevils to electron irradiation from a 1-Mev., peak, electron beam generator (106). Many other studies of lethal doses of ionizing radiation for insect species have been reported (6, 7, 37, 44, 45, 70, 117, 162).

Studies of botanical effects of electron irradiation on wheat seed showed that doses of 10,000 to 200,000 r.e.p. did not prevent germination, but wheat receiving 40,000 r.e.p. or more suffered drastic reduction in emergence from soil, and plants that emerged died soon thereafter (126). Radiation doses of the level required for insect sterilization were detrimental to early growth. Differences in baking quality were detected due to irradiation of wheat at higher exposures in this range, but were so slight that they would not be detectable using a commercial baking procedure (103). Other studies have also shown that ionizing radiation of the levels required for insect control would be satisfactory as far as milling and baking quality are concerned (8, 25, 33, 40, 79, 98).

Since ionizing radiations are so effective for controlling insects, and required radiation doses are not harmful to grain for consumptive use, practical applications have been seriously considered. The U.S. Food and Drug Administration has approved wheat irradiation for absorbed doses of 20,000-50,000 rads with gamma sources, providing energies of not greater than 2.2 Mev. (159). Electron irradiation of energies not greater than 5 Mev. is currently being considered for FDA approval (158).

Costs for gamma-radiation treatment to disinfest grain using Co-60 have been estimated in England (34, 36) at 3 s. per ton for continuous operation (37 cents per U.S. ton at $2.80-per-pound sterling exchange rate). This exceeds costs for conventional chemical fumigation, but costs of gamma sources are expected to decrease (35), and preliminary cost data on high-capacity electron accelerators appear promising for commercial treatment of grain (36).

Studies of gamma irradiation of citrus fruit also showed that low doses of radiation were effective in controlling eggs and larvae of the Mexican fruit fly (Anastrepha ludens (Loew)) (27). The FDA is also considering approval of gamma irradiation for citrus (158).

Design of gamma-radiation facilities for treatment of grain and citrus fruit to control insects has been considered by several investigators (26, 35, 36, 79, 160). A pilot-scale (2-1/2 tons per hour) Co-60 grain-irradiating facility is being installed for studies on insect control at the U.S. Department of Agriculture Stored-Grain Insects Laboratory at Savannah, Ga. The operating principle is such that it can be "scaled up" for design of commercial-sized installations. Since costs of radiation treatment will become more competitive as the technology progresses and because of health hazards from chemical insecticides, it is likely that ionizing radiation from isotopes and electron accelerators will be used to treat large quantities of grain and other products in the future.

Other possible uses proposed for ionizing radiation, perhaps further in the future, include a portable nuclear reactor for sterilizing soil in the field (150). Remote control operation could reduce the shielding requirements, and it is estimated that such a reactor could be built for soil treatment to control nematodes, insects, fungi, and weed-seed germination at much less than the present per-acre costs for required chemical control (150). Another report suggests that a 100,000-rad gamma-radiation treatment of soil would be sufficient to effectively inhibit weed growth as well as sterilize insects or nematodes and destroy a high percentage of the bacteria and fungi (21). Effects on beneficial soil bacteria would have to be taken into account, but perhaps complete sterilization followed by inoculation with the desired bacteria might be possible.

SONIC AND ULTRASONIC ENERGY

Sound and ultrasound, which are forms of radiant energy other than electromagnetic and particle radiations, have also received much attention for pest-control possibilities. Sonic and ultrasonic energy is propagated through air or other materials by means of a mechanical vibratory wave phenomenon associated with pressure differences in the medium. As with electromagnetic radiation, the frequency and wavelength determine the characteristics of the radiation. The range of audibility for humans falls within the 20- to 20,000-c.p.s. frequency range. Vibrations above the human auditory response limit are termed ultrasonic.

Uses of sound and ultrasound for pest control can be considered in two general ways: (a) By applying intense energy levels, which cause death directly by heating, damaging vital organs, or inducing fatal audiogenic seizures (4, 41, 57, 58, 60); and (b) by using lower intensities, to which pests respond somehow, to affect their behavior in some desired way. Killing pests directly with high-intensity sonic and ultrasonic energy appears impractical for a number of reasons (57, 58, 60). First of all, costs of producing the required energy are prohibitive. Also, intense energy levels can be maintained only in a restricted space, and so there is a problem of attracting the pests to the energy source. Further, if they could be collected, there would probably be more economical means of killing them. Using sound and ultrasound to influence behavior of pests therefore offers more promise for practical pest control.

Insect-Control Possibilities

An understanding of the ways in which insects use sound is important in attempting any control based on use of sound. Sound production and reception, as well as uses of sound by insects, have been studied extensively (3, 15, 61, 63, 144). These uses include communication, such as calling, congregation, and courtship songs, and alarm or distress sounds. Insects also use sound for protection. Some insects mimic other insects and some issue defense noises to discourage predators. They also use sounds from sources other than their own to detect predators and other dangers. On the other hand, some predators locate their insect prey through the calling sounds of the insects (143).

In their use of sound, many insects employ not only frequencies audible to humans but much higher frequencies as well. For example, songs of some species include frequencies up to at least 100 or 150 kilocycles per second (kc.) (61, 69a). Responses have been obtained from tympanic nerves of moths with stimuli of 240 kc. (119). Many studies have been conducted on the complicated and intricate calls of insects (3, 61, 69a), and modern electronics equipment has been employed in analyses of these sonic and ultrasonic signals (3, 61, 69a, 82). Sounds of different species were found to have specific characteristics (3) and can be used for identification purposes (82).

Possible applications of acoustic energy for insect-control purposes have recently been reviewed (15, 57). Some insect species have been attracted with artificial sounds and recordings of their own calling songs (15, 57, 61). In attempts to control mosquitoes, males were successfully attracted and killed with electric grids, using recordings of the female flight sounds (61), but the method was not successful for control because few males are required tc maintain the reproductive capability of the population (57). Other studies in attracting mosquitoes showed that a fundamental sine-wave tone attracted males as well as recorded flight sounds of the female mosquito when the sine-wave frequency matched the dominant tone of the female flight sounds (151). Studies by the same investigators also indicate that the mosquitoes use a phase principle in orienting to a sound source rather than a Doppler principle or an intensity-gradient-sensing method (152).

There has been speculation that flies may react to sound, but studies have been very limited and inconclusive (22, 57). Because of insecticide problems with dairy cattle, studies of the influence of sound on flies have recently been initiated by the Agricultural Research Service, U.S. Department of Agriculture.

Still other insect reactions to sound have been observed. Swarms of certain Diptera respond to sound (59). Swarms were startled by sounds with frequencies between 80 and 800 c.p.s. and gathered around the sound source only at frequencies near 125 and 250 c.p.s. Sound of sufficient intensity between 300 and 1,000 c.p.s. transmitted through beehives caused the insects to remain almost motionless, so that apiculturists could perform their work without using bee smokers (62).

No practical control measures using sound to attract insects have yet been developed, but there is need for further research on acoustical behavior of insects, from which practical methods for control might evolve (57).

Another acoustic response that is being investigated for control possibilities stems from the observation of evasive flight maneuvers that some moths perform when threatened with capture by bats. Bats emit sequences of ultrasonic pulses when flying and use the echoes to locate obstacles in their flight path. They also use this sonar system to locate and track flying insects. Studies have shown that bats emit these high-pitched chirps at the rate of about 10 per second and that the frequency of vibration is about 80 kc. (120). Extensive studies both in the laboratory and in the field have shown that certain moths detect the ultrasonic pulses of the bats and take evasive flight action to avoid capture by bats (120). The nature of tympanic nerve responses in moths was studied when the moths were subjected both to artificially produced sounds and those from flying bats. Flight patterns of moths in the field were photographed as the moths were exposed to batlike ultrasonic pulses. Reactions included abrupt and bewildering changes in direction, tight turns, climbs, loops, and dives to the ground. These observations have been confirmed by other scientists (15).

Further evidence that the moth flight reactions were due to acoustic stimuli was obtained by equipping insect light traps with ultrasonic sources and comparing insect catches with those of identical light traps that had no ultrasound equipment (15, 139). Recorded and imitated bat pulses and continuous ultrasonic energy at different frequencies were studied (15). Evasive flight of moths was observed due to the ultrasonic stimuli, and catches of moths in the ultrasonic traps were much lower. Among several factors noted in results of the experiments were differences in the repelling frequencies for moths with thoracic tympanic organs and those with abdominal tympana (139). In some studies the ultrasound appeared less effective in repelling insects during damp weather (15).

Because of the dramatic effects of batlike sounds on moth flight activity, studies are now underway at two locations at least to evaluate the principle for practical use in protecting crops from certain insects. Experiments in Ontario (15, 16) showed that broadcasts of batlike ultrasound over a plot of sweet corn reduced infestation by the

European corn borer by greater than 50 percent. While this method repels the insects rather than destroying them, if applied over a large enough area, the population might be reduced by modification of the mating and ovipositing behavior (16).

Laboratory and field studies on the effects of ultrasound similar to that used by bats are also underway in South Carolina to evaluate this principle for control of the cotton bollworm (Heliothis zea (Boddie)) (2). Studies of tympanic nerve response indicate a maximum response to ultrasonic stimuli in the frequency range from 21 to 27 kc. for this species (Taft, pers. commun., 1964). Responses of the tobacco budworm (Heliothis virescens (F.)) and the cabbage looper (Trichoplusia ni (Hübner)) are also being investigated as to effects of sound stimuli duration, frequency, pulse shape, and pulse repetition rate.

Further evidence that sound energy may affect ovipositing behavior of insects has been obtained recently in studies with stored-grain insects. Exploratory studies in which Indian-meal moths were continuously exposed to a low-level hum from loudspeakers during a 4-day oviposition period indicated a much lower emergence and poorer survival for insects from eggs deposited during exposure to sound (84).

The future of sonic or ultrasonic methods for insect-control purposes is difficult to predict. Certainly more research is needed in this area to better understand the effect of acoustic factors on the behavior of various species. Depending on the findings, sound and ultrasound may very well be among pest-control methods of the future. A phenomenon worthy of mention here has been reported on the auditory detection of modulated radio-frequency energy by humans (51). By some detection mechanism in the head, fairly weak RF electromagnetic fields were perceived as sound characteristic of the pulse modulation. To our knowledge this capability has not been observed nor looked for in insects. If some similar mechanism were active in insects whereby acoustic signals might be detected from modulated RF energy, the problem of transmission of acoustic stimuli would be greatly simplified.

Control of Birds

Sound also has been used experimentally and in practice to repel both mammals and birds (58); however, only work on birds is included in this paper.

For many years, pyrotechnic devices, carbide or acetylene exploders, and rifles and shotguns have been the principal sound sources used to repel birds. Research has shown that birds often can be repelled or crop damage lessened with use of pyrotechnic devices. Rockets, aerial flash bombs, and rope firecrackers were useful in protecting ricefields against red-winged blackbirds (Agelaius phoeniceus), grackles (Quisalus quiscula), and cowbirds (Molothrus ater) (100). The rope-firecracker technique when properly employed has been very effective in protecting rice (100) and sweet corn (101). Rockets are not used much today in the United States, probably because of high costs; however, 300- and 600-meter rockets are used with some success in Germany and Switzerland to frighten starlings (Sturnus vulgaris) from roosts and vineyards (28; Keil, pers. commun., 1962). Rockets generally are used with other sound sources, for example, gunfire, or distress calls. In England, rockets and aerial bombs have been used with shotguns to disperse starlings from roosts. Intensive efforts have cleared a roost by the fourth night (19).

The exploding shotgun shell (hereafter called the shell cracker), with a range of 100 yards, has been excellent for frightening ducks from grain fields (154). During the past 6 years, several hundred thousand shell crackers have been used in the United States to repel ducks and blackbirds from crop fields, starlings from roost sites, and many different species from airports (47, 125). In England, similar devices called "smoke puffs" have been used to frighten birds from airfields, but they usually have been combined with bird distress calls (23). Short-range shell crackers (60 meters) are used also in Germany at cherry orchards and vineyards, again usually with other devices (28). In Canada, 12-gage shell crackers have been compared with Very pistol flares and marine signal rockets, and though the tests were limited, the flares or rockets appeared to be more effective than shell crackers, since they left a trail of smoke or sparks (89).

Shell crackers have been widely used and are considered effective for flushing starlings if used regularly or in combination with other devices (156). Shell crackers also reduced numbers of herring gulls (Larus argentatus) feeding at garbage dumps in New England. Gulls were repelled from a dump at Chatham, Mass., for 8 days and from a dump at Portsmouth, N.H., for 6 days (81).

At some airports, bird problems have been alleviated by "shotgun patrols." Using both regular ammunition and shell crackers, patrol personnel fire upon nuisance birds. This system has worked particularly well at Logan International Airport, Boston, Mass. Several manufacturers in the United States are developing reliable, long-range (200 yards) shell crackers. Patrolling with noisemaking devices is one of the few effective methods, and the use of shell crackers is being encouraged, as well as the development of better types of ammunition.

Carbide or acetylene exploders have been used for bird dispersal for many years. These devices have been employed with varying degrees of effectiveness in fields of rice, corn, and grain to repel ducks, geese, and blackbirds (100). Carbide exploders in a small grain area in Saskatchewan reduced duck damage without spreading the losses among other farmers (130). Acetylene exploders and rope firecrackers were used to repel red-winged blackbirds from a Delaware cornfield during the 1961 damage season (93). Significantly less damage occurred when the scare devices were used, and the exploders were superior to the rope firecrackers.

In tests comparing exploders with broadcast alarm calls to repel red-winged blackbirds from an Ohio cornfield, both devices, operated on alternate days, offered significant protection (92). The exploder was effective to a distance of 600 feet. In California, two carbide exploders were used successfully to repel an estimated 5,000 starlings from two adjacent 5- and 20-acre fig orchards (156). No starlings fed in the orchards for the remaining 18 days of the experiment.

Carbide exploders also are used in France against Corvidae and other birds, but their effectiveness generally lasts only 2 to 6 days (124).

Rifles and shotguns are used widely against nuisance birds, both as lethal agents and as scaring devices. The .22-caliber rifle was reported as the best single weapon known for frightening blackbirds from open ricefields (100). Larger caliber rifles also are effective, but ammunition cost is considerably higher. The shotgun, although often used, was reported to be one of the most ineffective weapons against blackbirds attacking ricefields (100). Shotguns are used a great deal in England. They are believed to have little effect on bird numbers, but are effective as a scaring method (124). Shotguns used with other sound sources are also important devices for dispersing starlings from roosts in England (19), Germany (122), and Switzerland (99). With the advent of shell crackers, the shotgun also has become very useful, particularly at airports, where shotguns are considered safer than rifles.

In recent years, research workers have investigated the potential of ultrasonics, air horns, and broadcasts of recorded calls. Many individuals have expressed the idea that nuisance birds might be controlled with ultrasonics. The upper audible limit for birds is about the same as that of man, however (58); and hence ultrasonics offers little at this time for use in bird control.

Air horns effectively deterred starlings from feeding in a California vineyard. The horns were battery operated, and the rate of operation was automatically timed. Five horns, operated from 6:30 a.m. to 6:30 p.m. daily, were used to protect 57 acres of grapes for 7 days (156).

Frings and his coworkers have developed a relatively new and unique approach to the control of pest birds. The method employs recorded communication signals of birds to affect their movements. Starlings were chased from tree roosts by broadcasting a recording of what is now commonly called the distress call (55). Herring gulls were successfully repelled from feeding sites and attracted to other feed by using both alarm calls and feeding calls (54). Recorded calls of the eastern crow (Corvus brachyrhynchos) were also used to study reactions to broadcasts of assembly and alarm calls (53). Frings et al. concluded that biologically significant sounds may have practical value for attracting desirable species or for repelling pest species.

An active bioacoustics research program has been underway in France since 1950, when the Laboratoire de Physiologie Acoustique was founded. Emphasis is on research on acoustical bird distress signals and their practical application to agriculture. Fundamental research is being conducted on the semantics of a signal, its physical characteristics, species interspecificity, and the type of equipment required. Basic factors in the efficacious signals are being sought, particularly for the Corvidae and starlings. Present crop protection from birds in France is based almost solely on the use of distress calls. The techniques are the result of experiments conducted since about 1954. Cropland can be efficiently protected from rooks (Corvus frugilegus), jackdaws (Corvus monedula), and carrion crows (Corvus corone) for 2 weeks. An interspecific reaction has been observed in that the distress call of any one of these species will also protect the crops from the others. Distress calls have been used for as long as 2 months against Corvidae at a pear orchard without waning effects. When distress calls were used against nesting carrion crows for several days, the birds appeared to become disoriented--some left the nest and some sat beside the nest. A collection of eggs indicated that incubation had been interrupted (124).

Considerable research has been conducted in Germany since 1959 to develop acoustical methods for repelling starlings from vineyards and cherry orchards. German research workers report better success with two starling alarm calls they have recorded than with the distress call used by most other workers (Keil, pers. commun., 1962). During the 1961 damage season, starlings were repelled from 50 acres of grapes for 7 weeks by broadcasts of the two starling alarm calls (122). Six loudspeakers were used, and the cost of protection was $25 per acre. Starlings were also successfully repelled from an isolated 2-acre cherry orchard, but the problem of protection is considerably more difficult where orchard tracts are continuous and birds can move from orchard to orchard (Bruns, pers. commun., 1962). Starling distress calls have been used in combination with pyrotechnics to disperse starlings from fall roosts (Koenig, pers. commun., 1962). In England, starling distress calls have been used with limited success to repel birds from orchards and woodland roosts (124).

In the United States, the starling distress call has been used to repel starlings from seedless grape vineyards (20, 156[2]) and to discourage starlings from roosting in English holly (Ilex aquifolium) (155). Alarm or distress calls of the following species are now being used for alleviating damage in vineyards, cattle feedlots, and spring lettuce: House finches (Carpodacus mexicanus), red-winged blackbirds, yellow-headed blackbirds (Xanthocephalus xanthocephalus), Brewer's blackbirds (Euphagus cyanocephalus), robins (Turdus migratorius), and horned larks (Eremophila alpestris) (20). In other tests, birds were successfully repelled from a 14-acre feedlot during an entire damage period using amplified distress calls of a starling, adult female redwing, and adult female Brewer's blackbird, interspersed with a marsh hawk (Circus cyaneus) call. At another larger feedlot, tests using partial sound coverage combined with the use of poisoned bait were less successful (110). Distress calls of red-winged and yellow-headed blackbirds were broadcast from stationary units, a mobile truck-mounted unit, and a portable unit in an airplane in evaluation tests for repelling these species from corn (110). Results have been variable. Birds can be frightened from cornfields with the airplane-distress-call combination, but are persistent in returning. This control method does not appear to be economically feasible at this time for use in corn.

Broadcast distress calls of the black-footed albatross (Diomedea nigripes) and the Laysan albatross (Diomedea immutabilis), helicopter and other aircraft noises, pulses of random noise, and a series of pure tones were used on Midway Island to evaluate the relative effectiveness of various sounds as acoustic barriers to the Laysan albatross. Some success was reported in affecting the movements of flying albatross by using the black-footed albatross distress call and helicopter rotor noise. The authors stated that high-intensity, low-frequency noises appeared to hold promise for alleviating the gooney bird problem at Midway (52). Further research in the development of acoustical controls was recommended.

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[2] Research results by Zajanc (156) for air horns, bird distress calls, and shell crackers in vineyards and carbide exploders in fig orchards are based on a cooperative program with the University of California and the California State Department of Agriculture.

There has been much interest in evaluating the use of alarm and distress calls of several gull species commonly found in great numbers at certain airports. Gulls are involved in many bird-plane strikes and have caused much damage to aircraft. Experiments with gull distress cries began in Holland in 1956, and by 1958, loudspeakers had been installed along a runway at a military airport plagued by gulls. The distress calls of three species of gulls are broadcast just prior to takeoff. Hardenberg (pers. commun., 1962) reported that the system has proven extremely effective in reducing the number of bird-plane strikes. In France, black-headed gulls (Larus ridibundus) and herring gulls were effectively repelled from the Nice Airport from March through October 1963 using a sound truck (96). In England, bird distress-call experiments begun in 1959 were less successful than in Holland and France. Mobile sound trucks were used at airports, with limited success, to repel lapwings (Vanellus vanellus) and starlings. Success in repelling herring gulls was poor (Brown, Sugg, and Brough, pers. commun., 1962). Preliminary work with distress calls of ring-billed gulls (Larus delawarensis) and herring gulls in Canada indicated that distress calls should be useful in the dispersal of birds at airports, but that the calls probably will have to be reinforced with other frightening devices (89). The use of mobile sound units for certain airports is being considered in Canada.

During the past 2 years, gull distress calls have been tested by the U.S. Department of the Interior on gulls feeding at garbage dumps, on loafing gulls at airports, and on gulls on a breeding island. Varying degrees of success were achieved in modifying herring gull behavior and movements (81). Gulls at feeding sites (garbage dumps) were prevented from feeding for intervals ranging from a few hours to more than 12 days depending on the availability of alternate food supplies. Distress calls, augmented with shell crackers, appeared to be more effective than distress calls alone. Broadcast distress calls repelled gulls from breeding islands for only a few hours, but showed no loss of effectiveness in 8 days at an airfield.

Results of these studies indicate that the success of sound stimuli depends on how they are used and on environmental and behavioral factors. The effectiveness of broadcast distress calls and shell crackers for repelling herring gulls from feeding and loafing sites depends on the strength of the drive to remain in a feeding or loafing area (site tenacity) in relation to the strength of the reaction to the stimuli. Since the strength of these reactions changes with time and place, it is unlikely that the success of a given stimulus can be predicted for all situations (81). Care must be exercised when inferring success or failure of a particular experiment. Apparent success should be viewed with just as much suspicion as apparent failure. Factors to consider in determining the success of any repellent stimulus include the strength of the native reaction to the stimuli, the availability and suitability of alternate sites to which birds may be dispersed, site tenacity, the presence of abnormal or nonreacting individuals that act as decoys, weather factors, and the stage of the birds' annual cycle, i.e., migration, breeding, or wintering (81).

Results of work in various places indicate that nuisance birds can be repelled for at least short periods with a variety of sounds. Results have been particularly encouraging with broadcast alarm and distress calls, used alone or in combination with other stimuli. Most experiments in repelling birds have been conducted with no knowledge of the basic behavior of the species involved, however. Such studies are therefore very much overdue. Emphasis should be directed toward finding the strongest sound stimuli and the strongest combination of sound and other stimuli that will affect the movements of problem species. Practical use of acoustical bird-control methods will require cost appraisals as well as basic studies of life history, ecology, and behavior.

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EXPERIMENTS ON THE CONTROL OF INSECT POPULATIONS WITH LIGHT TRAPS

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The primary purpose of these experiments was to find ways of controlling the hornworms that attack tobacco without using insecticides.

The tobacco hornworm (Protoparce sexta (Johannson)) is a major pest of tobacco and tomatoes wherever these crops are grown in the United States. The tomato hornworm (P. quinquemaculata (Haworth)) attacks the same crops, but is much less numerous in most of the tobacco-growing areas.

These investigations were conducted near Oxford, N.C., in 1961-64. A description of the traps and data for 1961 and 1962 have been published elsewhere (Lawson et al. 1963 and Stanley et al. 1964). Additional data for 1963 and 1964 and from similar experiments are reported in papers now in press (Gentry et al. and Hoffman and Lawson). This is a general account of the entire investigation.

REVIEW OF LITERATURE

The biology of the hornworms was discussed by Gilmore (1938), Madden and Chamberlin (1945), and Metcalf (1909).

Frost (1952) reported that light traps had never been too successful in the control of injurious insects. He considered traps to be at best a supplementary measure. Much of the early work was done with daylight lamps or weak mercury-vapor lamps. In the 1940's the availability of improved lamps stimulated research on light traps, and several reports on the control of various insects were published.

Taylor and Deay (1950), working on the European corn borer Ostrinia Nobilalis (Hübner)) in Indiana, used seven traps along the edge of cornfields. These were electrocutor grid traps, some with 100-watt reflector mercury-vapor lamps and others with five 30-watt black-light fluorescent lamps. The population of borers was reduced 57.0 and 69.5 percent at distances of 153 and 87 feet, respectively, from the trap location. Damage from stalk breakage caused by the borers was reduced nearer the traps. This result substantially agreed with results of earlier work with light traps by Ficht, Hienton, and Fore (1940).

Pfrimmer, Lukefahr, and Hollingsworth (1955) found that four fan- and four gravity-type traps with black-light lamps were ineffective in reducing populations of the pink bollworm (Pectinophora gossypiella (Saunders)). There were indications that the traps were drawing the moths from distant parts of the fields.

Noble, Glick, and Eitel (1956) reported no control of the corn earworm (Heliothis zea (Boddie)), the pink bollworm, and the cabbage looper (Trichoplusia ni (Hübner)) in an experiment they conducted in Texas in an area covering about 3,000 acres where they operated 142 light traps. Clogged electrocutor grids sometimes caused the traps to fail because of electrical shorting and, thus, to lose effectiveness.

In experiments on hornworms, Morgan and Lyon (1928) found that amyl salicylate was attractive to moths, and they developed methods of using this bait to trap them. They reported that when six traps were placed in and around a 16-acre field of tobacco in Tennessee, the population of eggs and larvae was 2.63 per plant as compared with 6.67 in surrounding fields. The next year in a field with eight traps per 8 acres, there were 4.1 hornworms as compared with 6.3 in the controls.

Gilmore and Milam (1933), also working in Tennessee, tested the same attractant in devices containing sugar water and tartar emetic. Moths feeding from these containers were killed. Feeders were placed at different densities near tobacco fields in areas ranging from 9 to 25 square miles. The percent reduction in hornworm populations averaged 51.7 in 1929, 68.9 in 1930, and 53.7 in 1931. Scott and Milam (1943), again working in Tennessee, tested traps and poisoned feeders with the same attractant in a randomized-block experiment consisting of nine treated plots each 1 square mile in area. The results showed reductions in numbers of eggs laid amounting to 62.6 percent in trapped plots and 66.3 in baited plots.

Stahl (1954) tested bait traps and electric-light traps in North Carolina. He stated: "Field studies indicated that the use of either bait or light traps had little effect on the abundance of and damage caused by hornworm larvae on tobacco at or near the traps."

For 3 years in succession Stanley and Dominick (1958) placed three black-light traps on each of three tobacco fields of about 5 acres in Virginia. The average reduction in number of plants damaged by hornworms was about 16 percent.

Research has been conducted in southern Indiana on tobacco farms with favorable results. Traps are recommended in that State for control of hornworms on tobacco if placed so that the tobacco plants are within 110 feet of the traps with 15-watt black-light lamp attractant (Purdue University, 1961).

PRELIMINARY INVESTIGATIONS

Lawson et al. (1963) found that bait traps failed to catch hornworm moths before June 10, 1961, although moths were caught in light traps. Later in the season the catch of bait traps was very low compared with that in light traps. In the same year, these authors placed 14 light traps in a circular area having a 1-mile radius, with an additional trap 2.43 miles distant from the center. They then released 3,087 moths at the center of the area or about 2 miles from the center, and 3.0 percent were recaptured. There was no relation between distance from the point of release and the rate of recapture; the trap at 2.43 miles caught nearly as many moths as traps near the point of release. In one test, 218 moths were released within 50 feet of a trap; 42 (19.3 percent) were recaptured in this trap and 9 were taken in more distant traps.

From these results it was apparent that hornworm moths were traveling considerable distances and were not always caught when they flew within a few feet of a light trap. The comparatively high catch of marked moths in the most distant trap suggested that the low rate of recapture may have been because the area was so small that moths flew all the way through it without being captured. To test this, the same 14 traps were relocated in a much larger area at distances ranging from 0.89 to 4.36 miles from the release point, with six additional traps placed at various intervals ranging from 2 to 10 miles of the release point. In this test 4,582 marked moths were released and 11.7 percent recaptured. Furthermore, there was a definite relation between the distance of the trap from the point of release and the number recaptured.

Lawson et al. (1963) published curves showing this relation for males. The number of females recaptured was too low to give a significant regression, but the plot resembled the male graph. The regression equations were $\log \underline{Y} = 2.21531 - 0.4916\ \underline{X}$ for P. *sexta* and $\log \underline{Y} = 1.1314 - 0.1673\ \underline{X}$ for P *quinquemaculata*, where $\underline{Y}$ is the number of males recaptured and $\underline{X}$ is the distance from the point of release in miles. By substituting appropriate values in the equation, it can be calculated that the number of P. *sexta* males recaptured was reduced 50 percent with each 0.61 mile increasing distance. P. *quinquemaculata* was reduced the same amount in 1.80 miles. Many moths flew 3 to 4 miles in a single night. The greatest distance hornworms have been known to travel was 6.3 miles for two P. sexta males and one P. quinquemaculata female in 1961 and 8.1 and 8.2 miles for two P. sexta males in 1962.

It was evident from these data why previous attempts to control hornworms with traps on small areas had failed. Such areas would be subjected to a continuous influx of moths from outside, and only part of these would be caught.

The size of area required for a useful experiment can be estimated from the marking and recapture data, provided some allowance is made for the movement of moths over a larger and larger area as they dispersed from a central point. In correcting for the distance factor, it was assumed that moths dispersed at random and the effective range of all traps was the same and circular. If the diameter of this circle is "d" and the distance of a trap from the point of release is "r," then the catch of the trap should be approximately proportional to $d/2\pi r$. Since "d" and "2π" are constants, an approximate correction can be obtained by multiplying the catch by "r." If this correction is applied to the data for P. sexta males, the regression equation then becomes $\log Y = 2.003 - 0.266 X$, and the regression coefficient is highly significant. From this it can be calculated that 5 percent of a dispersing population will travel 4.89 miles. Then in a circle with a radius of 4.89 miles, 5 percent of the moths at the center will have come from outside the circle.

After estimating the increase in total catch to be expected from increasing the number of traps, it was concluded that about three traps per square mile were necessary to control the population of P. sexta.

Since a certain minimum area is needed to measure a population, the experiment as set up in 1962 consisted of two tangent circles, each 12 miles in diameter. The western circle had 6 light traps placed at about 1-mile intervals in each of four directions from the center outward, with a total of 24 traps in 113 square miles. The eastern circle had 324 light traps in an area of the same size, or about 3 per square mile. In addition, six traps were placed at about 1-mile intervals, extending out 6 miles from the outer edge of the eastern circle to the north, south, and east. The center of the eastern circle was 6 miles west of Oxford, N.C.

The size of the trapped area was increased to a circle 20 miles in diameter in 1964 and the legs were extended 10 miles beyond the circle, but this experiment was put into operation too late in the season to yield much useful data. Each trap was equipped with a 15-watt black-light lamp.

EFFECT OF LIGHT TRAPS AND STALK CUTTING ON HORNWORM POPULATIONS AND DAMAGE TO TOBACCO

Since it was not possible to count all the moths caught in all traps, moth counts were made daily or every 3 days in only 52 traps. These traps were located in four radii extending outward from the center of the circle, a distance of 12 miles in 1962 and 1960 and 20 miles in 1964. In 1964, the number of traps in which moths were counted was increased to 62.

When the data were examined, it was found that the numbers of hornworms caught per trap tended to be lowest at the center of the trapped area and gradually increased outward in all directions as far as the trap lines extended, although there were differences between species, sexes, and years. The data are illustrated in figures 1 and 2.

The same general pattern of distribution was also seen in counts of eggs made on 12 tobacco fields in 1962, 45 in 1963, and 48 in 1964 (fig. 3). For the first 2 years these counts were made on farmers' tobacco, which in many fields was treated with insecticides. Hence, although estimates of damage were made, no significant differences between damage in the light-trap area and that in the area outside the light traps could be established. In 1964, the samples were taken on half-acre plots of untreated tobacco. Figure 4 shows the number of plants attacked by hornworms. Again, the general gradient in extent of damage was the same.

There was a marked depression in moth and egg populations and in damage in the area covered by light traps. This depression extended for a considerable distance outside the area trapped. The reduction in populations

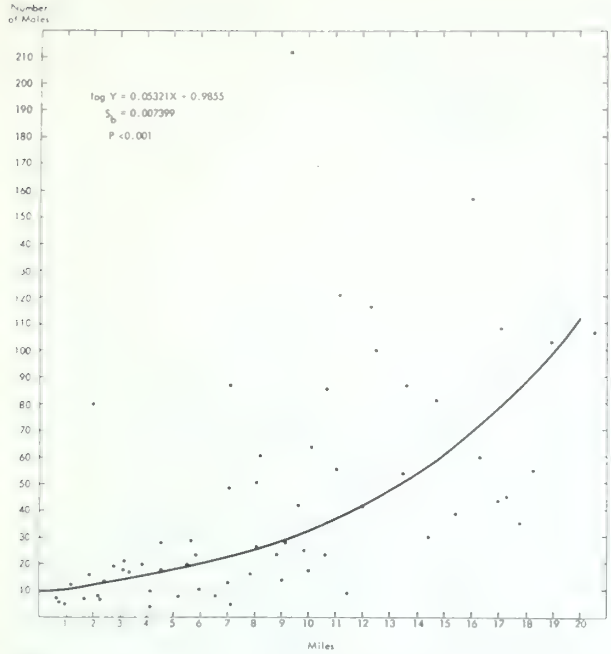

Figure 1.--Total number of male P. sexta moths caught in each of 62 light traps from May 28 to August 4, 1964, plotted against distance from center of trapped area.

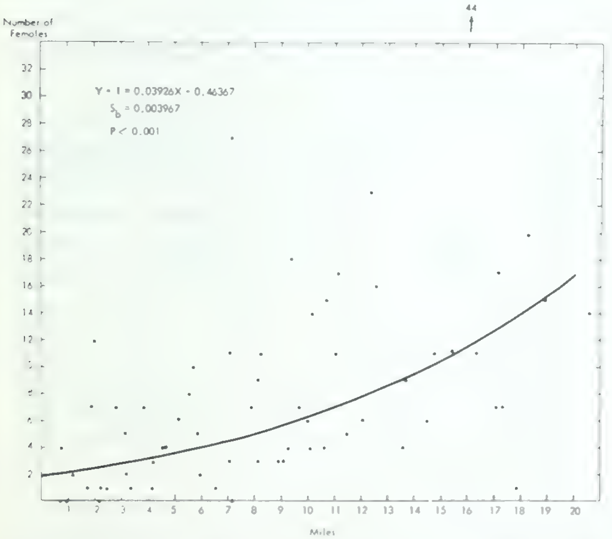

Figure 2.--Total number of female P. sexta moths caught in each of 62 light traps from May 28 to August 4, 1964, plotted against distance from center of trapped area.

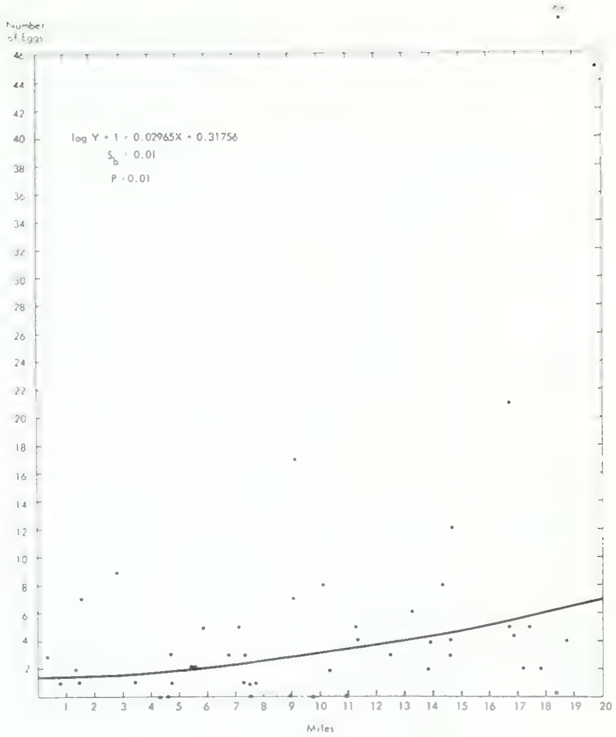

Figure 3.--Total number of hornworm eggs laid on 25 plants of tobacco in each of 48 fields from June 15 to August 6, 1964, plotted against distance from center of light-trap area.

might have been caused by the traps or by other factors.

The only known variable, other than the traps, that might have caused the depression was a difference in the number of tobacco fields producing the overwintering brood of hornworms. In the Oxford area, diapausing hornworms are found in tobacco fields in August before the crop is harvested and in September on suckers that grow on the stalks after the leaves have been removed. Early destruction of these stalks for nematode and insect control has been a standard recommendation for many years (Metcalf 1909). Nevertheless, surveys in previous years have shown that about 40 percent of the tobacco fields in the Oxford area are left undisturbed long enough to produce some overwintering hornworms on suckers.

The general survey made in the fall of 1961 covered only part of the light-trap area, and the data are not adequate to determine whether or not there were any differences between the area covered by light traps and the area outside. In 1962, there was a tendency for the number of stalk fields to increase from the center out to 14 miles. Fourteen percent of the fields remained inside the area as compared with 37 percent outside. There was evidence that farmers in the area had begun to

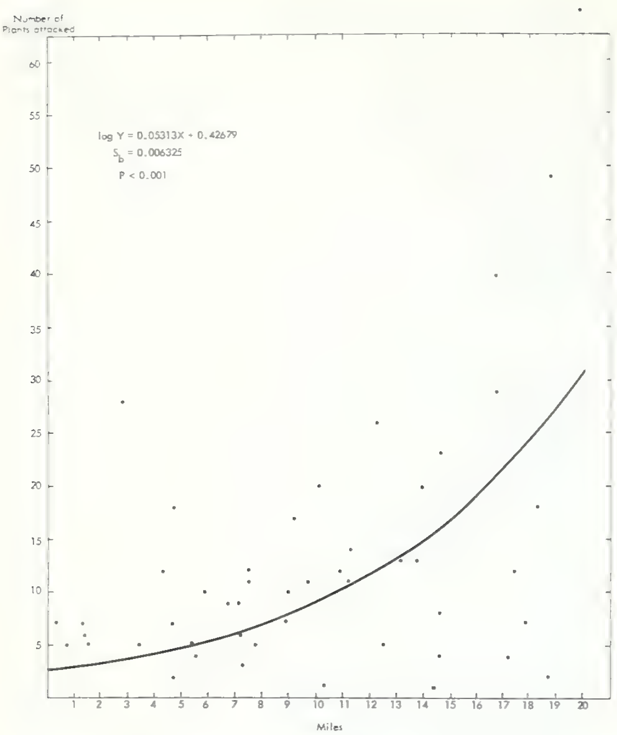

Figure 4.--Number of tobacco plants per 100 showing attack by hornworms August 18-22, 1964, in 48 fields not treated with insecticides, plotted against distance from center of light-trap area.

follow the standard recommendations and had increased stalk destruction partly as a result of our activities. Since it seemed better to have all the stalks cut rather than part of them, each grower in the fall of 1963 was urged to destroy all stalk fields before hornworm and budworm larvae were mature. Figure 5 shows the number of fields remaining.

The graph indicates that the distribution of stalk fields in this area resembled the distribution of hornworms and damage shown in the previous graphs. That is, if the hornworm populations were affected by the number of stalk fields, the effects of host-plant abundance and light traps were confounded in this experiment. It is not possible to separate the effect of these two factors because populations are not necessarily proportional to the number of fields.

Nearly all tobacco fields in this area were treated with a sucker-control chemical, and the suckers produced were mostly small and

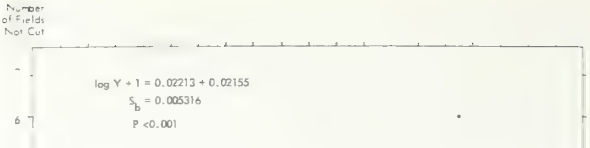

Figure 5.--Number of tobacco fields per linear mile not cut or plowed in four directions from center of light-trap area, September 1963.

unattractive to ovipositing hornworms (Rabb et al. 1964). Nematodes and disease further reduced sucker growth, so that in the area studied there were very few, if any, fields producing more than a few hornworms and no such fields were seen in fairly extensive surveys. On the other hand, there was a heavy reduction in insecticide usage in the light-trap area, so that before harvest the number of hornworms surviving treatment may have been greater inside the light-trap area. In any case, it is clear that light traps or stalk destruction or both produced major reduction in hornworm numbers in the area.

The degree of control might be estimated by comparing average values inside and outside, but this would give a biased estimate, since hornworm movements would reduce the difference between high and low-population areas. The movement factor can be partially eliminated by using the regression equations, representing the population gradient, to calculate populations at the center of the circle and at some point on the outside. Theoretically the outside point should be the place where the population levels off, but there is no evidence that the population did level off at the farthest point sampled. We have arbitrarily chosen 12 miles for the outside point, since this is the same distance outside the light-trap area as the center is inside. The results of these calculations are given in table 1. Since counts were made in 1964 out to 20 miles, we have shown percent reductions out an additional 6 miles for this year for comparison.

Table 1.--Estimated reduction in average catch per trap of hornworm populations and damage at center of light-trap area from population and damage at 12 miles out from center

Year	P. quinquemaculata		P. sexta		Eggs laid	Plants damaged
	Males	Females	Males	Females		
	Percent	Percent	Percent	Percent	Percent	Percent
1962	89	59	76	55	58	--
1963	84	65	94	64	83	--
1964	--	--	77	75	71	77
1964[1]	--	--	89	86	82	89

[1] Based on 18 miles.

The reduction in hornworm populations was reflected in a reduced use of insecticides. In 1963, the number of applications made against hornworms was reduced by 90 percent inside the light-trap area as compared with outside. In 1964, there was a reduction of 55 percent in applications made against all insects.

In 1963-64, tobacco farmers in the light-trap area were told that the light traps were experimental and that they should apply insecticides to control hornworms as needed. The sight of large numbers of moths in the light traps created an unusual amount of interest in the traps among the local townspeople, as well as among the tobacco farmers. This stimulated the farmers to examine their tobacco fields more frequently than usual. Since these frequent examinations usually revealed very low hornworm infestations (table 1), most of the growers withheld insecticide applications.

EFFECT OF LIGHT TRAPS AND STALK CUTTING ON OTHER INSECTS

In 1963, counts were made of the numbers of corn ears damaged by the corn earworm (Heliothus zea (Boddie)) and the fall armyworm spodoptera frugiperda (J. E. Smith)). There was a small but significant difference of about 17 percent between the area covered by lights and the area outside. Counts were also made at 50-foot intervals in cornfields where a light trap was located in or on the edge of a field. There was a depression of about 50 percent within a few feet of the trap, but this leveled out to zero at about 300 feet.

In 1963 and 1964, counts were made of the number of budworms (Heliothis virescens (Fabricius)) and H. zea found on tobacco plants and the number of plants damaged. No counts of larvae were made in 1963 and differences were not significant in 1964, but there was a significant reduction in damage. Again, when results at the center of the area were compared with those 12 miles out, the reduction was 92.9 percent in 1963 and 55.8 percent in 1964. As with hornworms, it was not possible to separate the effect of lights from that of stalk cutting.

IMPROVEMENTS IN LIGHT TRAPS

Some experiments have been run using variations of the basic trap, which utilizes a 15-watt vertically mounted fluorescent blacklight lamp and four baffles (see fig. 6). This design was developed from several others employed in earlier experimental hornworm trapping work in Virginia, Indiana, and other tobacco-producing States. Limited studies during 1963 with other traps equipped with a suction fan and greater lamp wattage showed no improvement in hornworm catches. The addition of a fan to the basic trap did increase the catch of corn earworm moths 138 times in one experiment and 1.89 times in another.

Hoffman and Lawson (in press) ran a series of experiments in which virgin females, which

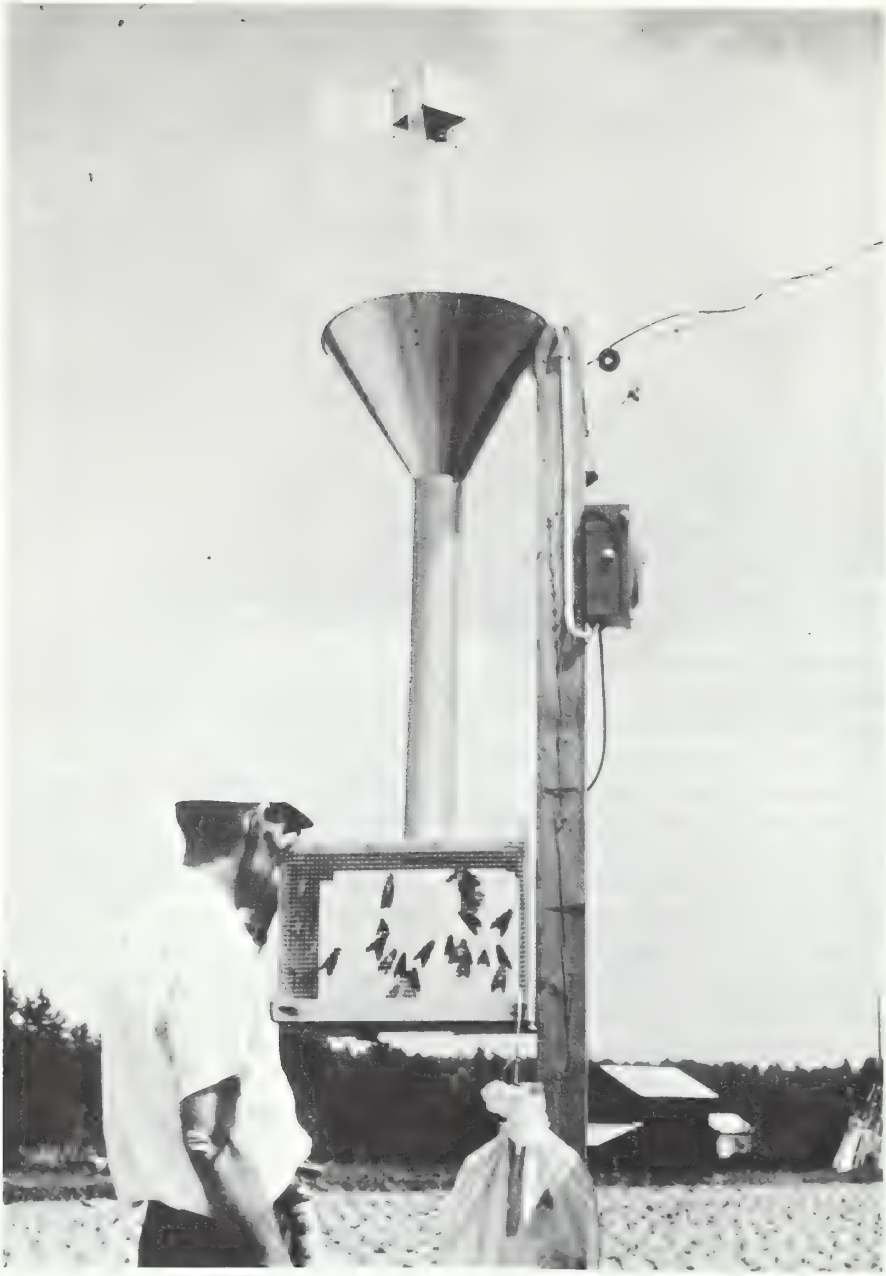

Figure 6.--Basic light trap, installed near Oxford, N.C., is representative of more than 360 such traps operated in 1962-64 to control tobacco hornworms.

produce a substance attractive to the males (Allen et al., 1962), were kept in small cages near light traps. The traps were located at least a mile apart and varying numbers of females rotated between locations. Table 2 shows the results of the first experiment. There was a significant increase in both male and female catches. For unknown reasons, the increase in female catch was not repeated in later tests, but male catches were always greatly increased. Figure 7 shows the effect of increasing the number of virgins. If it is assumed that the catch of the light trap alone is 100, then the regression equation will be $\underline{Y} = 100 + 94.3\ \underline{X}$. That is, one virgin female will approximately double the catch of a light trap;

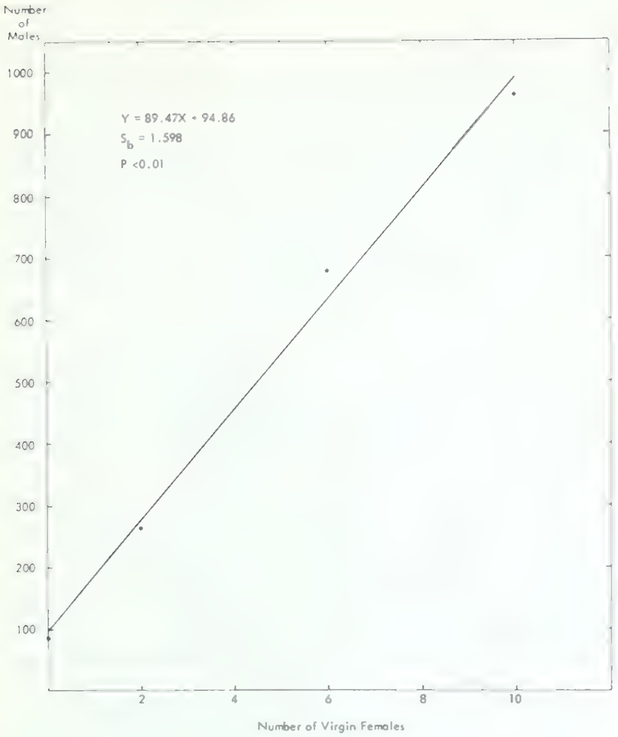

Figure 7.--Number of male *P. sexta* moths caught in light traps when virgin females were held in small cages at trap. Females were rotated between trap locations so that each location received all treatments.

Table 2.--Comparative catches of *P. sexta* in light traps with and without virgin females held in a small cage inside trap. (4 replications.)

Virgin females	Average moths per trap per day	
	Males	Females
Number	Number	Number
0.............	20.25	4.37
4.............	[1] 111.50	[1] 9.62

[1] Differences in catches of both males and females are significant at 5-percent level by F test.

two will triple it, etc. However, in a later experiment the number of virgins was increased to 30, but the catch was increased only 25 percent.

In the large light-trap experiment, the comparatively high reduction in males did not affect the fertility of the females. However, the very large increase in male catches when virgin females (or an equivalent amount of attractant) are added might well do so, particularly if the males caught can be sterilized and released.

In conclusion it may be said that, although further work will be necessary to test these methods in other localities and to determine more exactly the contribution of different factors to the total reduction in numbers, there is no question that hornworm populations and insecticide usage on tobacco can be much reduced. These results also suggest that, although any one population-control measure may not be enough by itself, the use of two control measures may be highly effective and much cheaper than insecticides.

SUMMARY

Previous tests of light traps for the control of various insects have generally shown these devices to be ineffective except at short distances. At Oxford, N.C., in 1961, marking and recapture data indicated that numbers of hornworms (*Protoparce sexta* (Johannson) and *P. quinquemaculata* (Haworth)) might be reduced by traps if the area were large enough. In 1962, a test was set up with three traps per square mile in a circular area 12 miles in diameter. In the first year, the number of females per trap was reduced more than 50 percent and males more than 75 percent at the center of the area as compared with 6 miles outside. In 1963 and 1964, interpretation of the results was complicated by an increase in cultural control in the area. The reduction in moth populations was greater in these years, and the numbers of eggs laid on tobacco, damage to the crop, and insecticide usage decreased from 70 to 90 percent. Populations of other insects were also affected.

In experiments using variable numbers of virgin female hornworms in small cages near light traps, each female up to 10 caused the catch of males to increase by an amount approximately equal to the catch of males in the light traps alone.

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ROLE OF AGRICULTURAL ENGINEERS IN PEST CONTROL

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Research on the engineering phases of pest control cannot be effective without well-organized cooperation with appropriate scientific disciplines and agencies (18). Agricultural and other engineers are cooperating with other disciplines whenever and wherever the situation and resources permit. Therefore, let it be clear at the outset that, although this discussion will be primarily about the engineering phases of pest control, we are convinced of the need for a balanced team effort among the disciplines involved on any specific program.

From a long-range viewpoint, research should be encouraged on the development of methods other than chemical for at least the more important pests. In this class would fall such methods as the use of natural biological agents and attractants, resistant crop varieties, cultural methods, sterility procedures, physical measures, sanitation and management of storage and processing plants, and insect-proof packaging for products subject to insect attack in storage.

Chemical or mechanical weapons, or the cultural and sanitary measures that we have always used to mitigate insect damage, can often supplement the beneficial effects of natural insect diseases, parasites, and predators to provide adequate economic control. A physical method could be used to reduce an insect population, so that extremely small amounts of an insecticide would be enough to "mop up" an infestation (23). It is apparent that the development of chemicals selective in action on specific pests, as well as improvements in ways to apply pesticides, would be important in the use of such measures.

Although nonchemical methods for pest control are intriguing, they also have weaknesses. Entomologists have shown that parasites and predators have adjusted over the years to a balance with their hosts such that they kill some but not all of them. Complete host destruction would eliminate the parasite or predator by destroying its food supply. Thus, control of the pest is seldom complete enough to prevent economic damage. Furthermore, reduction of the pest population is rarely sufficient to prevent its becoming dense again. An insect host may become resistant to a natural enemy just as it may develop resistance to chemical controls (29). Therefore, we will expect to rely generally on supplemental chemical treatment of the infected plant or animal for many years to come (5).

Individuals in industry have long been aware of need for "ideal" application of pesticides, but they still admit to having only a broad concept of the job their application equipment is supposed to do (10). We in the research field have not yet told them the optimum deposit pattern for control of specific pests with particular chemicals. The development of pesticide application techniques and equipment should parallel the work on chemical development (17). Ideally, the pesticide, its application techniques, and, if needed, special application equipment should become available to the user simultaneously. Unfortunately pesticides are developed, recommended, and sold without adequate research on application equipment or techniques.

Certain assumptions may be made with respect to reduction of the residues from chemical application (18). Of course, the ideal solution to reduce residues is elimination of the need for chemicals (14). But if chemicals are to be used, only the minimum amount for optimum control should be used (23), with application of the right kind of chemical in the right place, at the right time, in the correct amount, and properly distributed for the needs (9).

Improved equipment to deposit chemicals in predetermined locations not only would increase the effectiveness of pesticides but also would reduce substantially the amount needed for optimum control. This, in turn, would reduce the cost to farmers and reduce drift and residue hazard to man, animals, beneficial insects, and crops. Although present equipment and techniques of applications have resulted in substantial gains to agriculture, methods are still relatively crude and application efficiency is low.

Development and design engineers are hampered in creating and producing more efficient equipment for applying chemicals by the lack of basic knowledge about the behavior of materials during and after application (1). Increased basic research is needed to determine the complex effects of physical factors on the movement of chemical particles from the time they leave the applicator until they are deposited. In addition to the size of particles and droplets, these factors include aerodynamic and inertial effects, gravitational and electrical forces, and temperature gradient effects.

Despite out acknowledgement that several disciplines should be concerned with pesticide application, we believe that many of the physical and engineering aspects can be considered in isolation from entomological, pathological, and crop-production problems, provided these aspects are treated in general terms. We will, therefore, limit our discussion to consideration of these aspects.

PUBLIC SERVICE RESEARCH

Research for the determination of basic equipment requirements for given sets of conditions can frequently be conducted more effectively and at lower cost by the public research agencies because of facilities already available for other fields of research. In many cases, private or cooperative interests may not be justified in undertaking research where the costs may be more than the pioneering company can recover. There is also the possibility that the net return from the sale of new or improved equipment may be no more or even less than that of the machines replaced (20). Industry, particularly the smaller manufacturers, must invest its limited research and development money in projects that will bring relatively short-range monetary return. Since public service agencies can justify projects on the basis of potential improvement in the standard of living and health, much more basic and longer range projects are usually justifiable. Over a period of years, the public has come to realize the necessity of this long-range research, and it is being carried out extensively in both the universities and the U.S. Department of Agriculture. Industry is anxious to cooperate in any way possible in basic or applied research that enables it to advance closer to the common object--that of the public good.

BASIC ENGINEERING RESEARCH

The primary purpose of basic engineering research in pest control is to gain information on fundamental principles, which is ultimately made available to applications research and to manufacturers as an aid to the development of techniques, equipment requirements, and the execution of final designs. For example, U.S. Department of Agriculture research studies deal with topics of interest in pesticide application ranging from droplet generation, counting and sizing, and dispersal through particle diffusion in turbulence and the characterization of particulate deposits on solid surfaces. A brief survey of some of the research studies will be given, with a description of some special facilities.

Automatic Scanning

A flying-spot particle analyzer has recently been constructed by Airborne Instruments Laboratory, Long Island, N.Y., under contract for the Agricultural Engineering Research Division of the U.S. Department of Agriculture. The instrument is designed to scan negative photomicrographs of solid particulates or liquid droplets, which are prepared on 35-mm. high-contrast film. In addition to the normal functions of counting and sizing, special logic circuits are incorporated in the instrument to perform lineal analysis. The measurement functions included are (1) size distribution and count of intercepts across particles; (2) size distribution and count of distances between particles; (3) total scan area covered by all particles; (4) total scan area represented by the space between the particles; and (5) count of particles on two boundaries of the scan field. The last measurement has statistical value in compensation for edge-effect errors when a large number of adjacent fields of a large area are scanned.

The particle analyzer sizing calibration is fixed with respect to the film, but the corresponding physical particle dimensions being dealt with in the measurements are dependent only on the microscope magnification used in micrograph preparation. The micrographs must have the highest possible contrast between particle images and the intervening matrix to insure adequate detectability. Similarly, the best possible focus must be maintained over the entire area to be scanned on the micrographs to insure the greatest possible sizing accuracy. Optimum accuracy of the particle analyzer is realized for circular particle images, although the instrument is designed to handle micrographs of irregular particles.

Several techniques have been used for particle and droplet sampling for the particle analyzer. Two techniques for collection of liquid droplets are (1) use of glossy paper or processed photographic paper, as done by Fumidge (12), and (2) collection in an immiscible fluid spread on glass microscope slides, as discussed by Sharp and Bufton (22). Both methods have depended on the use of a dye in the atomized liquid to obtain sufficient photographic contrast. The photographic paper technique results in very suitable particle images and is convenient to use except for the disadvantage that spread factors must be determined if droplets are to be measured. For large droplets, low magnification photography or even contact photographic printing of the sample paper is adequate.

By the technique of the immiscible fluid collection medium, it is possible to capture the droplets in spherical, liquid form, and no spread factor determinations are necessary. The most successful adaptations of this method have involved the use of two collection-fluid layers, the upper and lower layers less than and greater than, respectively, the specific gravity of the atomized liquid. With this arrangement, droplets are trapped at the fluid interface. In the case of solid particle sample preparation, the work to date has involved simply dispersal of solid particles on glass microscope slides by standard methods. Normally, extra care is given to assure a minimum of particle agglomeration during dispersal owing to the serious effects in particle size distribution determination by automatic scanning.

In optical photomicrography for automatic scanning, the large amount of light usually transmitted by fine particles and the inherently short focal depth present considerable problems. Hence, the technique originated by Hamilton and Phelps (13) is utilized. After the particles are suitably dispersed on a mciroscope slide, a negative image of the dust deposit is prepared by vacuum evaporation of metal at normal incidence onto the slide. When the slide has received a precise, natural-size impression of the geometric projections of the particles, the particles are removed. Transparent profiles or holes in the metal film remain as "shadows" cast by the particles. The technique is applicable only to samples where the particles are deposited directly on the slide without the use of an adhesive material. Since the metal film is at most only a few hundred angstroms thick, a sharp plane of focus is provided for the optical microscope. Adjustment of film thickness aids attainment of the desired degree of contrast in the ultimate photomicrographs. Copper has been found to be a very satisfactory shadowing metal, since it exhibits no objectionable structure effects in optical photomicrography. Certain particulate substances are sometimes difficult to remove subsequent to the shadowing process, and work is underway to deal with this problem. Among the removal methods being investigated are the application of air and water jets, as used by Hamilton and Phelps, the use of wetting agents, and ultrasonic treatment.

Either transmitted or incident microscope illumination may be used for the metal-shadowed specimens where, under visual observation, particles appear as bright areas in a dark field or as dark areas on a bright field, respectively. Although the particle analyzer is capable of measurements of either dark particles on a light field or the reverse, ultimate selection of the illumination method rests upon the quality of photomicrographs obtained.

Attempts are being made to use automatic scanning on electron micrographs of clay particles. Particles are dispersed on a specimen screen and shadowed at relatively shallow incidence by means of chromium evaporation; the particles are left in place subsequent to shadowing. After preparation of micrographs in an electron microscope, photographic procedures are used to further enhance contrast and to reduce images to dimensions compatible with film requirements of the particle analyzer. Although some degree of success has been obtained, much further work is indicated before the methods can be considered suitable.

Diffusion of Particles in Turbulence

At the U.S. Department of Agriculture Pioneering Research Laboratory on Physics of Fine Particles, theoretical and experimental studies are in progress on the behavior of fine particle suspensions in fluids. The basis and elements of the approach used are discussed by Pasquill (21) and Sutton (24), and are briefly outlined here.

Most of the early theoretical treatments of turbulent diffusion have been based on the phenomenological mixing-length or transfer theory, as developed by Prandtl and others. In such theory, a partial differential equation, similar to the ordinary diffusion equation, is used to describe the particle dispersion process. The counterpart of the usual diffusion coefficient is a parameter termed the eddy diffusivity, or exchange coefficient. A large difficulty, particularly in the case of atmospheric diffusion, has been to adequately describe the variation to the eddy diffusivity, which occurs with respect to position (e.g., elevation) in the atmosphere.

However, a factor of more critical importance is that modern investigations in turbulence and turbulent diffusion have made clear more serious shortcomings in the transfer theory. For example, the transfer theory of turbulent diffusion assumes that a gradient-type diffusion prevails in the turbulent fluid, which does not necessarily follow in the light of statistical theory. Also, diffusion and convection of turbulent energy are not negligible, as the phenomenological theories presume. On the other hand, although the phenomenological theories are not completely satisfactory from a more modern research point of view, they are at present the most useful in practical applications. Since the statistical theories have come under more intensive investigation recently, they have not yielded a body of knowledge that has replaced the mixing-length theories in the applications.

The statistical theories of homogenous turbulence and turbulent diffusion originated in the pioneering work of Taylor (25, (26). In addition to the work of Taylor (27) and many others, important fundamental developments of the mathematical theory of turbulent diffusion for both the single- and the two-particle fomulations were set forth in two papers by Batchelor (2, 3). The statistical theories of turbulence and turbulent diffusion have been the subject of intensive investigation since the end of World War II.

In U.S. Department of Agriculture research in this area, a problem to be given attention is the turbulent diffusion in boundary layers, owing to its importance in determining the structure of surface deposits. Studies of boundary deposits of particulate matter encountered in such situations will be made with the aid of the previously described particle analyzer and a fluorescent racer method.

A continuous scanning technique is under development for use with fluorescent tracers to determine whether a conceptually useful characterization of an aerosol deposit distribution may be obtained. Visible fluorescence from the tracer material, which is excited by a beam of ultraviolet radiation, is collected by a microscope as a test surface moves past its objective at a constant rate. Appropriate primary and secondary optical filters suited to the ultraviolet source and the tracer are included in the optical path. The continuous scanning apparatus is not particularly sensitive to individual particles but responds in an integrated manner to the number of particles instantaneously in scan. The fluorescence is sensed by a photomultiplier system and the output signal is recorded on magnetic tape. Since the studies to date have been limited to (statistically) homogeneous deposits, an apparently stationary random signal is recorded as an output. Therefore, the signals will be analyzed by the techniques of generalized harmonic analysis, which are suited to such applications, just as is done in the analysis of turbulence. Both digital and analog techniques will be available for data processing.

It is likely that two types of continuous scanning will be necessary: (1) A low magnification system intended to scan over relatively large distances and larger scale deposits and (2) a high magnification microscope scanning system for more detailed investigations of small-scale deposits on limited areas. In addition, it is reasonable that discrete results obtained from uniformly spaced samples of aerosol deposits measured by standard chemical methods will be amenable to similar analyses by digital computer. The particle analyzer will be employed in more detailed studies, with ordered sequences of readings being subjected to a digital analysis in order to examine spectra or correlations. By means of suitable responsive anemometry equipment, studies will be made of the associated turbulence field to examine the relationships between turbulence and deposit structures.

It is appropriate to speculate about some of the implications of particle diffusion studies being carried out in several places with respect to pesticide application. For example, (1) a more meaningful and useful description of fluid transport processes near plants, in the atmosphere, and in application devices should be possible; (2) studies of pesticidal drift should be greatly aided, and the ability to predict drift distribution may be enhanced; (3) the ability to economically describe distribution of pesticide material on surfaces down to perhaps the microscale likely will be greatly developed; (4) deeper insight may be gained into relationships among force fields, turbulence and air flow character, and deposit structure; and (5) it should be possible to use even more efficiently deposit and residue analyses and to state more firmly about spacing of samples in making such measurements.

ENGINEERING

Industrial Application

Although industry engages in basic as well as applied and development engineering, it must, as one industrial engineer puts it, carefully consider for each machine a characteristic that may be described as its "degree of practical accuracy" (10). The machine must "pass the economic test," which permits it to distribute pesticides at a cost that will allow their economic usage.

The objective of applied engineering research in pesticide application is to develop new and improved equipment and methods for accurately directed and more uniform application of all types of pesticides--liquid, dust, granular or biologic--to all important crops and animals. The successful culmination of such research will reduce also the danger of damage to crops or wildlife on adjacent areas, will improve the control of pests, and will reduce the cost to the producer. Engineers will give increasing attention, together with their cooperators, to developing much more specific information needed on many aspects of present control programs. There are urgent needs for improvements on application methods and equipment to obtain better performance with less chemical and to reduce drift of the applied pesticide from the target site. There is a trend toward more use of highly directed applications of pesticides, e.g., the increased use of band application of herbicides in row crops. Substantial improvements can and must be made in application equipment, but more information must be obtained through research before these can be effected.

Deposit Specification

The first thing that must be known either accurately or approximately is how much chemical is required and where and how it is to be applied. Work by the U.S. Department of Agriculture during World War II indicated that there was an optimum size of aerosol for use in some insecticide spray applications. Work by the U.S. Forest Service indicates that certain drop sizes yield the best results for some types of forest insect spraying. Other research has shown that by directing the spray correctly, effective insect control may be obtained with greatly reduced dosages. In the final analysis, very little is recorded on research in deposit specifications--much more is needed.

Particle Size

It is useful to assume that a pesticide has a definable toxicity. In actual practice, we apply many times the amount of insecticide theoretically necessary to kill the insects if the insecticide could be distributed directly on the insects so that each insect received the minimum lethal dosage. It is interesting to calculate the number of insects that could be killed by 1 pound of insecticide if ideally distributed. For example, U.S. Department of Agriculture entomologists indicate that an "average" boll weevil may weigh approximately 17 mg. and that 1 p.p.m. of a good phosphate poison is required to kill it. Since the approximate amount of poison required to kill one boll weevil is $\frac{2}{100,000}$ mg. then 1 pound would kill approximately 23 billion weevils. Assuming a plant population of 23,000 plants per acre, we could kill 1,000 boll weevils per plant on 1,000 acres. Even more startling calculations could be made for much smaller insects, such as the mosquito and the aphid, but such results only lead to wrong impressions, since no field-application procedure will approach these efficiencies.

It is well known that the forces on a particle depend on its size. It is also generally believed that biological effectiveness of a pesticide often depends on the size of particles into which it is divided. This conclusion is usually based on calculations of the theoretical coverage obtained from dividing a specified volume into particles of various sizes. Table 1 shows how 10 gallons of liquid would cover a perfectly flat surface, with droplets having a contact angle of 90°.

From these figures it is not difficult to appreciate the reasoning in favor of low-gallonage fine-droplet spraying. However, although it has been assumed that pest control generally improves as we divide our pesticides finer and finer, experimental evidence does not completely confirm this supposition. We are certain that, quite often, the finer the droplets the more difficult it is to control their placement.

Only a few years ago row crops, such as potato and tomato, were being sprayed at application rates varying between 100 to 200 gallons per acre and with pump pressures from 300 to 400 pounds per square inch. With these high-gallonage applications, there was less reason to be concerned about the size of the spray droplet than with the mist sprays, which often are used at the present time (30).

Table 1

Drop diameter (microns)	Drops per square centimeter	Mean distance apart	Amount of 1 acre covered at contact angle - 90°[1]
	Number	Mm.	Percent
10	2,213,500	0.00683	266.0
20	267,000	.0194	133.0
40	33,350	.0547	66.5
75	5,600	.134	35.5
100	2,135	.217	26.6
200	267	.610	13.31
400	33.3	1.74	6.65
750	5.6	4.24	3.55
1,000	2.13	6.83	2.66

[1] For plant surfaces, these figures would have to be divided by the acres of plant surface per acre of land, which may vary from 5 to 20, and then multiplied by a spread factor corresponding to actual angle contact.

In one project (30), several series of experiments were carried out in which spray-droplet mass median diameter could be varied by chosen increments, usually 100 microns each, from 100 to 500 microns. (Mass median diameter represents a measurement that means that 50 percent of the volume of the spray is contained in drops of less diameter than the stated diameter.) Throughout a series of experiments extending over 10 years, these research tests demonstrated that, on diseases of potatoes and on potato and tomato insects, virtually any combination of pressure and volume that was used to obtain spray droplets between 100 and 500 microns gave approximately the same control.

Other research (11) has indicated that foliar applications of herbicides tended to be more effective as the herbicidal formulations were decreased from 0.3 mm. down to 0.1 mm. in diameter.

It appears that in the future there may be a greater tendency to try to control the size distribution of pesticide particles (15). The development of granular materials is an example of this, because it was seen that it was easier to make the particles behave in a certain way when they were of a relatively narrow particle-size distribution. Many processes that affect the behavior and the deposition of pesticide particles depend in some way on particle size (15). For example, the smaller a pesticide particle the greater will be the aerodynamic drag forces compared with its inertia and the less will be its deposition from inertial impaction; the greater will be the thermophoretic repulsion from surfaces; and the more one may have to depend, e.g., upon electrostatic or other effects instead of gravity to obtain deposition. As a result, it may be difficult in certain cases to obtain anything resembling precise control of particle application if we attempt to deal with an assortment of sizes, which may have a 200-1 range, such as in a conventional spray.

The process that primarily has controlled spray and dust deposition in our past equipment has been inertial impaction, i.e., the projection of a pesticide cloud in the direction of the plant. Since this process is so widely used, it is surprising in retrospect that so little work has been done on it from an agricultural point of view.

A method of pesticide application of interest to, and under study by, several industrial and research organizations is the electrostatic charging of pesticide particles. Experimental results have indicated that, under cetain conditions, a significantly greater amount of material will be deposited on the plants when particles are charged. Several companies are now manufacturing dusters that use electrostatic charging as a means of improving deposition. Some of the dusters are undergoing testing, whereas others have been put into use. Further research is indicated to obtain a better picture of the way in which this force may be used.

Electrostatic, gravitational, and thermal forces and inertial effects need to be explored over a wide range of particle-size distributions and turbulence conditions with various kinds of particles, including dusts, sprays, and fogs. The attainment of any significant increases in pesticide application efficiency will depend on the knowledge of how to control and to apply these forces and effects.

Measurement and Evaluation

The problem of measuring chemical distribution is one of our most critical because all other research hinges upon it. This will include high-speed quantitative measurement of particle distribution on plant surfaces and mass measurement of chemical distribution on and in the soil. Until we have these methods available, all other research on pesticide application equipment will have a corresponding lack of precision.

Accurate and rapid measurement of particle-size distributions is quite difficult, and relatively little has been done in this field. Most measurements have been made by direct microscopic particle sizing and counting. This is a tedious and expensive procedure and is subject to error as well, both in sizing and in sampling. Other sizing methods, such as air classifiers, sedimentation systems, and light-scattering and electrical sensing instruments, have been applied. In the U.S. Department of Agriculture, as previously indicated, an automatic scanning method will be used to study the details of particle distribution on surfaces, as well as in the determination of particle-size distributions.

It would be helpful to be able to compare the biological effectiveness of different application methods and the physical performance of the various machines. Biological differences might then be identified with physical differences, which might be common to several methods or machines or both. If an important effect was found to be general, a principle could be established that could be utilized in other situations. However, the biological effect of an insecticide, for example, is in part dependent on the distribution of the insecticide on or in the insects, and this is rarely measured. We only infer that the insecticide is available whenever the insects die and vice versa.

Rapid and accurate methods for calibration and for estimating the efficiency of pesticide application equipment are still needed and are not readily available. Individuals attempting to develop better methods and equipment for pesticide application, including the biological specialist who wishes to observe the toxic effects, need to take dozens and perhaps hundreds of samples of deposits on and around the plant, animal, or other object being treated. There may be a need to make rather difficult quantitative analyses of the amount of material on each sample in order to get a measure of the performance of a single pesticide application method (15). Various new methods for measurement of pesticide deposition have been proposed, including fluorescent tracers, chemical tracers, and radioisotope activation analysis. Engineers are frequently bothered by the fact that they do not have good statistics on the percentage of pesticide that actually reaches the plant or even the principal types of spraying equipment used on the major crops. The difficulty in obtaining a quantitative measurement of any new improvement in application equipment is obvious when that of present equipment is scarcely known.

The only really practical method of determining equipment performance in the field would be one that would provide a nearly instantaneous numerical reading of the deposit on a group of targets placed in selected locations. With such an instrument, one could analyze the deficiencies of present equipment and could compare the effectiveness of various technique and equipment modifications. If such an instrument, or set of procedures, is ever realized, it will probably be the result of public service research, since the amount of investment industry can afford to make on this type of work is restricted (10).

There is every likelihood that as time goes on the need will be for greater and greater precision of application, not only with chemicals but with other methods, such as biological control. Insect viruses have been tested as a means of controlling cabbage loopers, corn earworms, and the tent caterpillar. Such applications may need to be extremely precise, since, for example, a man could hold on his fingernail enough cabbage looper virus concentrate to treat 5 acres.

Aerial Application

Research today indicates that spray discharged along the lateral axis of an aircraft will follow the airflow set in motion by its passage through the air until the accompanying forces will no longer support the spray droplet. The airplane develops three principal airstreams, which affect spray distribution: The two wing-tip vortices and the propeller vortex. These vortices, plus the effects of gravity and atmospheric turbulence, determine the path of the pesticide discharge and the resultant deposit pattern. Although it is obviously impossible to eliminate propeller and wing-tip vortices, at least with today's airplanes, research is underway by public and private agencies to develop a new type of airplane configuration that will permit much better control of aerial pesticide application and of pesticide drift. The airplane is now virtually a standard agricultural implement, and improvements will continue to be made for this activity.

We are only beginning to understand the airflow effects surrounding the helicopter, but research is underway to determine under what conditions it will be more or less suitable than a conventional aircraft in pesticide application. The Agricultural Engineering Research Division of the U.S. Department of Agriculture now has available one helicopter, from which are being developed experimental data that we hope will be of considerable usefulness.

Granular Materials

Seldom has a farming practice had such rapid acceptance as the use of granular insecticides and herbicides. Many farmers are now practicing chemical weed and insect control utilizing granular materials and equipment. The desirable characteristics of application vary with the crop, the insect, and the chemical used.

Ideally, the discharge from a granular applicator should be proportional to the ground speed, but, because of the nature of the materials, no completely satisfactory type of metering device has yet been available (16). As more selective and more toxic chemicals appear, greater accuracy will be needed. For example, for corn borer control, spreading devices that will apply granules in 14- to 20-inch bands directly over the corn plants are recommended. For soil insect control, granules are dropped directly out of the discharge tubes for both band and overall applications. As with other equipment, the specifications for control need to be established so that equipment can be developed to fill the need.

Granular insecticides can be applied by hand as, e.g., has been done in orchard tests, where the soil under trees was treated with aldrin granules (28). However, the economical application of granular insecticides over large acreages naturally requires the use of power-driven spreaders. More specific machines and attachments need to be developed as, e.g., in the case of preemergence herbicides or soil insecticides, where application of less than 90 percent of the recommended rate can result in ineffective control and application rates higher than recommended can be costly or may injure the crop (4).

Particulate Spray

An interesting new approach to the reduction of pesticide drift pertains to the development of controlled drop sizes, according to the particulate spray concept (7). In this process, a water solution is imbibed by particles of a polymer known as a "particulating agent," whose particles subsequently swell to many times their dry volume, yet they do not dissolve. If the swelling capacity of the particulating agent added to the solution is just equal to the solution volume, essentially all the spray solution will be immobilized in the swollen polymer particles. The minimum size of swollen particles is governed by the dry size of the particulating agent employed. The particulated solution is then spray applied.

The mechanism of action postulated for particulate sprays suggests that an optimum amount of particulating agent in a solution would leave little solution free to form very small droplets. Consistency of the solution then should be directly related to effectiveness in reducing spray drift potential. Tests have shown that the spray produced has much less volume of small droplets than does a comparable solution containing no particulating agent. Particulate sprays have effected a major reduction in drift in each test, but quantitative correlation was not possible, because the particulate spray reduced drift to a point beyond the detection level of the sensitive assay method employed in the field experiment (7).

Another interesting attempt to decrease spray drift is brought about by increasing the viscosity of the spray liquid by producing a water-in-oil emulsion, popularly known as an invert emulsion. This method helps to reduce the number of small droplets in sprays.

Soil Fumigation

A special case of pesticide application relates to subsurface application of pesticides for control of diseases or soil-located insects. Several of the soil fumigants are extremely corrosive, and engineers must provide proper structural materials resistant to corrosion. Some highly volatile fumigants must be retained in the soil by polyethylene covers, and special precautions must be followed in development of equipment, as some of the materials are very toxic.

Attraction of Insects With Audible and Ultrasonic Sound Waves

A recent report (6) describes an investigation of the tendency of sound and ultrasonic radiation to attract the ordinary house fly. Radiations from 180 to 40,000 c.p.s. at two intensity levels were used in the trials. The results of the experiment indicated that the insects did have sound responses, but further investigation is necessary before recommendations can be made.

It has also been reported that sound has been effective in repelling rats, mice, and other rodents. For example, a small unit with a frequency range from 17 to 26 kc. per second was reported to protect an area up to 40,000 square feet. A built-in system continuously shifts frequencies, so that the rodent will not become accustomed to one particular frequency.

Special Problems

One of the earliest means for insect control was the application of tillage techniques to reduce grasshopper infestations. Before the advent of good pesticides and pesticide application equipment, deep plowing was recommended to help prevent serious grasshopper infestations. Stubble fields were tilled in strips, so that more favorable egg-laying conditions existed in specific areas, which were subsequently given the proper tillage treatment to reduce the insect population.

Flame cultivation of some crops, particularly cotton, is effective for controlling weeds and thus results in the application of less chemicals. Eradication of weeds in cultivated crops by flaming is now standard procedure in some areas (30). Different kinds of plants are able to withstand amounts of heat depending on their stem structure, age, size, and shape. The intensity and volume of the flame and duration of exposure are important factors in attaining effective results. Detailed experiments have been carried out to determine the temperature patterns resulting from different experimental burners, which are then modified to produce more efficient flame nozzles.

Engineers have experimented with infrared radiation for rice drying and steam conditioning of tobacco in a vacuum to destroy insects in the stored commodities.

Although we generally think of pest control with respect to the principal farm operations, there is a major job to be done with respect to engineering in the development of equipment for the application of pesticides around the home (8). The home gardener and the individual who takes care of his lawn and shrubbery are greatly concerned with techniques and equipment for control of pests. One writer (8), suggests, perhaps with tongue in cheek, that one of the biggest single handicaps in weed control is the complete lack of really first-class pictures. He takes a rather jaundiced view of the usual pictures in lawn weed-control bulletins, since the home gardener must be able to identify them before he is able to ask for the proper herbicide. Having determined the best pesticide or herbicide, he is then confronted with the alternatives of equipment, all of which are rather inadequate.

It is extremely difficult for the home gardener to put on the recommended amount of insecticide when he has no ready way or means of determining how much he is applying. In some cases, such as the application of pesticides and fertilizers to the lawn, it is extremely difficult to know where the previous row of application was made. Suggested remedies for these problems have included fluorescent additives that will glow or bright colors that will stain temporarily.

The problem of markers is not peculiar to the home gardner. The aerial applicator who is applying pesticides to commercial fields of crops or to forests is confronted with an even more difficult problem, since he must be able to orient himself rapidly at high speeds of flight.

A Look Ahead

One who attempts to predict the direction for future research, engineering or otherwise, must understand that his guesses will be somewhat uncertain, particularly if he attempts to predict very far ahead. The rapid rate of progress in biological controls within the last few years and the fundamental information being gained with respect to insect and plant-disease characteristics will most certainly result in engineering tasks requiring a high degree of originality and imagination.

Hardly any of us remember when hand application of pesticides was the practice in the United States. However, in foreign countries probably more acres of crops are treated with hand equipment than with power equipment (19). It has been reported that insects in Mexico and Peru often are controlled by applying dusts or granulars by hand. As improved methods of control are developed, these areas will change their application techniques. For example, it was reported (19) that no pesticide was used in Ghana on cocoa until, less than a decade ago, an enterprising pesticide supplier entered the market by having a team of technicians show the Government how to spray cocoa and indicate the advantages associated with pest control. The result was a $4-million sale of pesticides. Also, Ghana imported 60,000 motor-driven knapsack sprayers in 1 year, and the order for 1964 was 25,000.

EXAMPLES OF APPLIED ENGINEERING RESEARCH ACCOMPLISHMENTS

The following items, although only examples, illustrate some of the past accomplishments of engineers, including agricultural engineers, in pest-control equipment.

Equipment has been developed for mist-concentrate spraying. Extensive research has shown that heavier deposits of toxicants can be placed on fruit and foliage with this method than with dilute-type sprays. Also, less total toxicant is normally required.

A versatile sprayer-duster, recently developed, holds promise for use on several low-growing row crops and has been used successfully against aphids on potatoes in Oregon and Washington. With booms that trail on the ground, the unit applies the pesticide to both the top and the bottom of the plant and permits farmers to apply wet or dry chemicals as needed.

Research has been done on animal-actuated units for pesticide application on cattle. They apply spray uniformly and distinctly reduce pesticide residues, as well as save spray material and labor.

For cotton, experimental equipment has been developed for picking up and destroying fallen, punctured squares to aid in the control of early-season buildup of the boll weevil. Preliminary results indicate that equipment has distinct possibilities as part of an overall control program for the boll weevil.

Basic research is being devoted to determining the particular wavelength of light to which insects respond. As a result, electric-light survey traps are now probably the most effective way of determining insect infestation buildup, which, in turn, dictates the need for initiating other control methods. In some cases, it may be even possible to utilize electric lights as attractants for partial or complete control of certain insects. Extensive installations of light traps have been made by tobacco farmers in Kentucky, North Carolina, and South Carolina during the 1964 season, and a rather large acreage of cotton will be covered during the 1965 season in Texas.

The efforts described are in line with other projects intended to improve both ground and air equipment for applying chemicals more precisely so that pests may be controlled more efficiently without adversely affecting growing plants or animals. Primary emphasis is being given in many projects to elimination of pesticide residues, including the reduction of drift. Rapid methods of measuring pesticide deposits are continuing to be developed and investigated. The development of granular pesticides for insect and weed control has been especially helpful, and their use for pest control is expanding so rapidly that it is now unusual to find a pesticide that is not available in granular form.

These are only a few examples of productive work, and the opportunities for useful physical and engineering research, as progress is made, will increase rather than decrease.

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